HABITAT RELATIONSHIPS OF SPRUCE GROUSE

IN SOUTHEAST ALASKA

by

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ABSTRACT

A geographically disjunct subspecies of spruce grouse, the Prince of Wales spruce grouse (*Falcipennis canadensis isleibi*), occurs on only a few islands in southeast Alaska. Other than limited morphology data, the scientific literature lacked any information on habitat relationships, ecology, and natural history of this subspecies. Moreover, no field studies had been conducted on spruce grouse in a temperate rainforest ecosystem. Thus, habitat relationships could not be readily inferred from the existing literature because the temperate rainforest of southeast Alaska is distinct from other ecosystems in the range of spruce grouse.

Spruce grouse were studied on Prince of Wales and Heceta Islands in southeast Alaska from April 1996-January 1998. Nineteen birds were captured and fitted with radio transmitters. Grouse were radio-tracked throughout the year with an emphasis on collecting data during the reproductive period. Habitat data were evaluated at 3 spatial scales (home range, core area, location) using logistic regression. A logistic model was fitted at the smallest scale of resolution, individual locations. Spruce grouse selected bog and high-volume, old-growth forest habitat and avoided clearcuts. Second-growth forest (15-30 yrs after clearcutting) and scrub forest habitats were used in proportion to their availability. No grouse, however, used large areas of second-growth forest exclusively, indicating that uniform structure may not be suited to all life requisites. Horizontal diversity may be an important component of spruce grouse habitat in southeast Alaska. Forest management practices which encourage horizontal diversity, avoid large patches

of uniform structure, and allow connectivity of natural patches across the landscape would be less likely to isolate populations of Prince of Wales spruce grouse.

I examined 2 aspects of reproductive ecology including: (1) invertebrate abundance as it relates to habitat use by brood females; and (2) microhabitats at male display areas and nest sites. No differences were detected in invertebrate abundance among 3 habitat types: bog, scrub forest, and high-volume, old-growth forest. However, means of invertebrate abundance and brood female habitat use exhibited a similar pattern. Both exhibited higher means in scrub forest habitat type. Experiments with more power are needed to determine if this pattern is real. Microhabitats at nest sites, measured by tree density and basal area, did not differ from random sites. Male display areas exhibited higher tree density than random sites, although no differences were detected in basal area measurements. These microhabitats, nest sites and male display areas, appear widespread within the landscape and would not likely pose limits to Prince of Wales spruce grouse populations.

I also studied several aspects of natural history for Prince of Wales spruce grouse. Home range characteristics and male courtship displays were described. Mean home range size (95% utilization distribution) for 13 adult and yearling spruce grouse was 211 ha with no differences between males (n=4) and females (n=9). Mean size of core areas (50% utilization distribution), a measure of breeding season use, was 34 ha. The breeding season distribution and observed estimate of overlap were used with suitable habitat data for an approximate density estimate: 3 birds/100 ha. Male Prince of Wales spruce grouse use the wing-clap courtship display characteristic of Franklin's grouse (*F. c. franklinii*). Prince of Wales spruce grouse males restricted displays to trees and did not display on the ground as did Franklin's grouse. The volume of sound produced by the wing-clap could be heard from approximately 30m and did not serve to indicate position through the dense, temperate rainforest vegetation.

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CHAPTER I

PRINCE OF WALES SPRUCE GROUSE

Introduction

A geographically and genetically isolated subspecies of spruce grouse (*Falcipennis canadensis isleibi*) inhabits a few islands at the southern extremity of the Alexander Archipelago in southeast Alaska. The exact distribution of Prince of Wales spruce grouse in the temperate rainforest of Southeast Alaska is unknown, as small (< 20,000 ha) islands in the region have not been inventoried. However, the grouse is absent from the Queen Charlotte Islands to the south, islands of the Alexander Archipelago to the east, and the adjacent mainland. The closest other spruce grouse, the Franklin's grouse (*F. c. frankilnii*), occur in drier habitats east of the Coast Range in British Columbia (Boag and Schroeder 1992).

The core area of spruce grouse sightings is from central and northern Prince of Wales Island (Figure 1.1). Other sightings have occurred on islands immediately adjacent to northern Prince of Wales Island (Gustafson 1993). Spruce grouse are most commonly observed along the dense logging road systems of Prince of Wales and Heceta Islands. Although density is unknown, the paucity of documented sightings of Prince of Wales spruce grouse potentially suggests lower densities than for Franklin's grouse through much of their range.

Until 1982, a single museum specimen represented spruce grouse from southeast Alaska (Osgood 1903). A recent examination of 6 additional specimens revealed

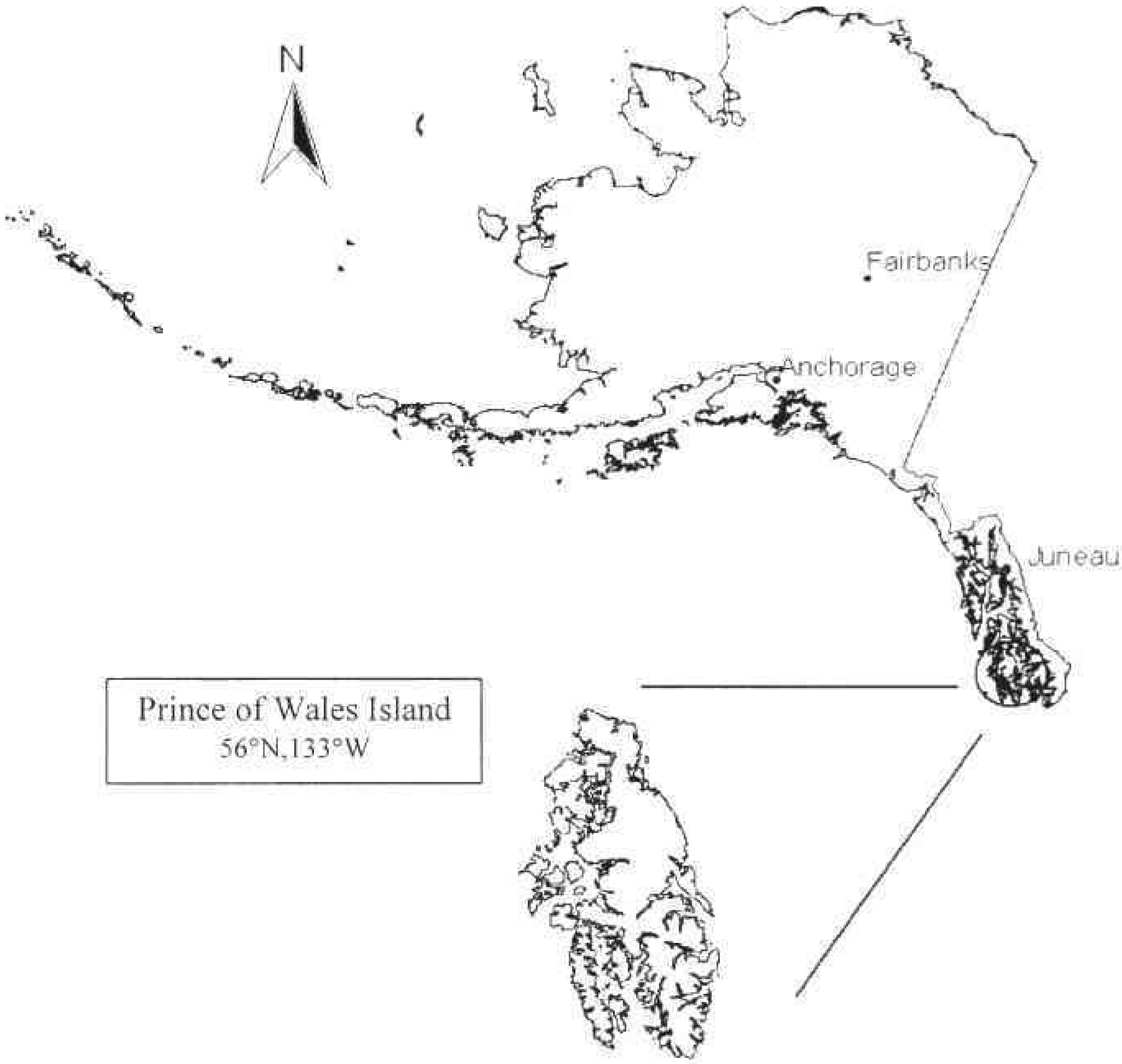

Figure 1.1. Location of Prince of Wales Island, southeast Alaska.

morphological characteristics distinct from mainland Franklin's grouse and warranted new classification: the Prince of Wales spruce grouse is considered a new subspecies (Dickerman and Gustafson 1996). The scientific literature held 3 minor references to this subspecies (Osgood 1905, Swarth 1911, Gabrielson and Lincoln 1959) until Dickerman and Gustafson (1996) initiated taxonomic work.

This investigation of Prince of Wales spruce grouse marks the only field study of spruce grouse in a temperate, rain-forest ecosystem. Marked differences in forest structure, forest disturbance patterns (rate and frequency), and climate in southeast Alaska indicated that habitat relationships for Prince of Wales spruce grouse could not be readily inferred from existing literature on other spruce grouse subspecies.

Background

The spruce grouse, a transcontinental species, exhibits different habitat relationships across its range (Anderson 1973, Haas 1974, Ellison 1975, Fritz 1979, Keppie 1979, Hedberg 1980, Robinson 1980, Johnsgard 1983, Allan 1985). In the northern and western (except southeast Alaska) portions of its range, fire and insect defoliation drive landscape dynamics (Keppie 1997). Large-scale patches are created by low-frequency, high intensity disturbance patterns (Picket and White 1985). Spruce grouse populations in the northwestern portion of their range reach highest densities within young successional stands of fire-sere ecosystems, because birds are distributed relatively continuously across the landscape (Boag and Schroeder 1992, Keppie 1997).

In the eastern range of spruce grouse, coniferous forests occur in a matrix of deciduous hardwoods and spruce grouse populations are often isolated (Fritz 1979). Along the southern border of their range, islands of coniferous habitat have resulted from anthropogenic changes to the landscape (Robinson 1980, Boag and Schroeder 1992, Keppie 1997). These spruce grouse populations have declined substantially and have been locally extirpated (Robinson 1980).

Spruce grouse population dynamics are, therefore, potentially distinct within the different portions of their range: some populations exhibit continuous, dense distributions and other populations occur in isolated patches. Thus, spruce grouse populations should respond to changes in landscape pattern (whether anthropogenic or natural) differently across their range (Keppie 1997). Where spruce grouse are distributed in small, isolated patches, populations likely function as some form of metapopulation, with population persistence dependent on 3 primary factors: (1) interpatch distance; (2) dispersal ability; (3) number of patches (Harrison 1991, Stiling 1992).

The habitat of Prince of Wales spruce grouse shares few similarities with that of other subspecies. Differences in forest pattern, landscape disturbance, annual precipitation, and forest structure are especially notable. The relatively recent influx of large-scale, anthropogenic changes (forest harvest) to the landscape of southeast Alaska increases the complexity of the habitat relationships, because the scale of this disturbance is foreign to the ecosystem (Alaback 1982, Hanley 1993). Fire-influenced ecosystems, for example, are characterized by high-intensity, low-frequency disturbance patterns (Pickett and White 1985) while temperate rainforests of southeast Alaska are characterized by frequent, low-intensity disturbance (Demeo et al. 1992, Hanley 1993). Single tree mortality or small windthrow events produce small openings in the forest canopy and gap-phase regeneration occurs (Alaback 1982). Within the landscape mosaic, multi-cohort stands form with complex forest structure in the absence of fire and other natural catastrophic disturbance agents (Demeo et al. 1992). The associated forest structure exhibits high vertical and horizontal diversity.

Although no habitat data existed for spruce grouse in southeast Alaska at the time of this study, the United States Forest Service rated old-growth forest as a high-use habitat for grouse reproduction and foraging (USDA-Forest Service 1983). Conversely, second-growth sawtimber was hypothesized to be of no-use for grouse reproduction and feeding. Dense second-growth stands, characterized by total canopy closure (Alaback 1982), lack important structural features of spruce grouse habitat: ground cover for concealment, forage such as *Vaccinium* spp., and low-level branches for roosting. Early successional stages following clearcutting, however, were rated of moderate use for grouse feeding but of no use for reproduction (USDA Forest Service 1983). This investigation explores habitat relationships of spruce grouse in southeast Alaska and serves as a test of these hypotheses.

Objectives

This investigation focuses on the habitat relationships of Prince of Wales spruce grouse and examines aspects of reproductive ecology and natural history.

I. To determine habitat use and selection by Prince of Wales spruce grouse.

II. To examine 2 aspects of Prince of Wales spruce grouse reproductive ecology:

(1) habitat use by brood females in relation to invertebrate abundance;

(2) microhabitats associated with nest sites and male display areas.

III. To describe home range and natural history of the Prince of Wales spruce grouse.

Literature Review

A short literature review is also included so that this document will serve conservation biologists and forest managers in southeast Alaska as a reference on spruce grouse. In addition, a history of this unique subspecies (prior to this investigation) is described.

Spruce Grouse

The geographic range of spruce grouse (*F.c. canadensis* and *F.c. franklinii*) conforms closely to the transcontinental band of boreal coniferous forest. In the Rocky Mountain and Cascade Ranges, however, the southern limit of the species is north of coniferous forests suggesting other limiting factors. For example, competition with blue grouse (*F. obscurus*) has not been investigated (Johnsgard 1983). Populations have been greatly reduced in Michigan, Minnesota, Wisconsin, New York, Vermont, New

Hampshire, Maine, Ontario, Nova Scotia, and completely extirpated on Prince Edward Island (Robinson 1980, Johnsgard 1983).

Although the species is tied to coniferous forests, the type of forest community and corresponding structure varies across its range. Fire-dominated, jack and lodgepole pine (*Pinus banksiana* and *P. contorta*, respectively) forests are among the most common forest types (Schroeder and Boag 1991, Boag and Schroeder 1992), while the coastal forests of southeast Alaska may be the most unusual. Forest disturbance regimes of fire-sere ecosystems differ markedly from the gap-phase disturbance patterns of southeast Alaska (Demeo et al. 1992).

In studied portions of their range, spruce grouse preferred short needled conifers, particularly various species of spruce and pine for arboreal forage (Ellison 1966, Robinson 1980, Pendergast and Boag 1970, Schroeder and Boag 1991). The flowers and fruits of shrubs and forbs, fungi, invertebrates, snails, and grit were commonly ingested (Pendergast and Boag 1970, DeFrancesci and Boag 1991). Brood females led chicks to openings in the forest where protein requirements were normally met with invertebrates, fruits, and flowers (McCourt 1969).

During fall and winter, spruce grouse shifted to arboreal foraging of conifer needles (Hohf et al. 1987). Flocks of 2-30 birds were commonly formed in winter (Ellison 1972, Boag and Schroeder 1992). Ellison (1973) observed that fall and winter home ranges were highly variable: 3-159 100 ha. Short migrations, up to 11 km, between wintering and breeding ranges have been observed in southwestern Alberta, north-central

Alaska, New Brunswick, and Ontario (Ellison 1973, Herzog and Keppie 1980, Boag and Schroeder 1992).

Spruce grouse commonly nested in a depression at the base of a conifer tree (Keppie and Herzog 1978, Boag and Schroeder 1992). The nest location was centered within the female's home range, maximizing the distance to other territorial females and display sites of males (Herzog and Boag 1977).

In comparison with other tetraonids, spruce grouse have a small clutch size (Johnsgard 1983). Franklin's grouse had the smallest clutches, averaging 4.8 eggs (Keppie 1982). Ambient temperatures may regulate onset of egg laying, with cool, wet conditions causing delays (Johnsgard 1983). In southwestern Alberta, egg laying commenced around 30 May (McCourt 1969). After 23.5 days of incubation, the chicks hatched synchronously and left the nest within 24 hours (McCourt 1969). Broods subsequently broke-up in 70-100 days (Schroeder and Boag 1985). Haas's (1974) estimate of summer juvenile mortality, 55% for 3 years, was comparable with other tetraonids.

Several estimates of spruce grouse population density are available for mainland North America. The highest densities recorded, up to 50/100ha, are *for F. c. franklinii* in southwest Alberta (Boag and Schroeder 1992). Seasonal estimates for *F. c. canadensis* are 8-12/100ha in south-central Alaska (Ellison 1974) and up to 83/100ha in Ontario (Szuba and Bendell 1983).

Franklin's Grouse

Franklin's grouse has been considered the closest taxon to the unique subspecies of spruce grouse in southeast Alaska (Gustafson 1994). Studies on Franklin's spruce grouse are from relatively dry and/or fire-influenced ecosystems of British Columbia, Alberta, Washington, and Montana (Boag and Schroeder 1992). Habitat includes forest communities of lodgepole pine, mixed stands of Douglas-fir (*Pseudotsuga taxifolia*) and lodgepole pine, and mixed stands of lodgepole pine and Englemann spruce (*Picea englmanii*) (Stoneberg 1967, Keppie and Herzog 1978, Boag et al. 1979, Schroeder and Boag 1985, Ratti et al. 1984, DeFranceschi and Boag 1991). In Alberta, Franklin's grouse avoided dense forest stands, preferring more open stands of lodgepole pine where flight was permitted in the understory (McDonald 1968). In north-central Washington, however, density and basal area of Englemann spruce were higher in plots where grouse were flushed than random plots (Ratti et al. 1984). Uneven-aged, old-growth stands supported large diameter trees that were used as activity trees (Ratti et al. 1984). Activity trees may be used for feeding, loafing, roosting, territorial displays and vocalizations and may serve as an index to Franklin's grouse density in relatively homogeneous forest communities (Gurchinoff and Robinson 1972).

In feeding trials, Franklin's grouse preferred the high protein and digestibility of lodgepole pine needles to other conifers (Hohf et al. 1987). An important summer food source in southwestern Alberta was *Vaccinium* spp. from which stem tips, flowers and fruits were consumed (DeFranceschi and Boag 1991). *Vaccinium* was also an important shrub layer which may have provided insect foods and concealment from avian predators.

In addition to *Vaccinium*, fungi, vascular plants, invertebrates, and conifer needles were important foods in summer (Schroeder and Boag 1985). Invertebrates were a critical source of protein for galliform chick development (Bergerud 1988). In central Alberta, 3 Franklin's grouse chicks <1 week old had exclusively consumed arthropods (Pendergast and Boag 1970). Juveniles also consumed fungi and fruits, and began to eat conifer needles by August (Pendergast and Boag 1970, DeFranceschi and Boag 1991).

McDonald (1968) described the behavior of male Franklin's grouse during courtship; adult males established territorial boundaries at points of interaction with adjacent males, but boundaries were only vaguely delineated elsewhere within the home range. Aggressive behavior was characterized by tail-swishing, wing-claps, and rushing charges at trespassing males. Similar behavior also was exhibited during courtship displays with emphasis on the vivid eye combs (McDonald 1968).

The territorial behavior of female Franklin's grouse maintained dispersion (Nugent and Boag 1982). Beginning in mid-winter, females established individual breeding areas by responding aggressively to other females (Herzog and Boag 1977). They defended breeding territories with aggressive calling (cantus) and by attacking intruding females (Nugent and Boag 1982). This behavior was thought to force immigrant and yearling females into unoccupied territories and regulate density of females (Herzog and Boag 1977).

The behavior of female and young Franklin's grouse was characterized by mutual call and response (Schroeder and Boag 1985). Dispersal followed the gradual increase of distance between hen and chicks and deterioration of communication (Keppie and Towers

1990). Aggressive interactions between juveniles did not appear to elicit break-up of broods (Schroeder and Boag 1985).

History of the Prince of Wales Spruce Grouse

At present, 4 publications refer to the spruce grouse of Southeast Alaska, which was believed to be the Franklin's grouse before the work of Dickerman and Gustafson (1996). Osgood (1905) discovered the disjunct population of grouse inhabiting Prince of Wales Island in 1905. In addition, he described the first nest of the grouse in a temperate rainforest ecosystem. The nest, containing 5 eggs, was a depression in a bed of moss with a Sitka spruce (*Picea sitchensis*) sapling sheltering the nest (Osgood 1905).

A second publication is from the Alexander Expedition of 1909. They did not find the spruce grouse described by Osgood. Instead, they found fecal and feather evidence and information from local peoples (Swarth 1911). Evidence was compiled to suggest the occurrence of the Franklin's grouse on Prince of Wales and 2 outer islands. No evidence suggested the occurrence of Franklin's grouse on any of the islands adjacent to the mainland. Furthermore, the expedition found that the distributions of spruce grouse and blue grouse were mutually exclusive. Wherever the occurrence of spruce grouse was suggested, they failed to hear the conspicuous hooting of blue grouse found elsewhere in the Alexander Archipelago (Swarth 1911).

Gabrielson and Lincoln (1959) considered the Franklin's grouse a rare bird in southeast Alaska that was closely associated with the spruce timber. These minor references prompted Gustafson (Alaska Department of Fish and Game) to compile specimens of the Prince of Wales spruce grouse for morphological analysis (Dickerman and Gustafson 1996). Prince of Wales spruce grouse, *F.c. isleibi*, exhibited white-tipped, upper-tail coverts and lacked a chestnut tail band, marking the major differences from *F.c. canadensis*. It also differed from *F.c. franklinii* by having shorter wings and longer tail. In addition, male plumage was darker in the Prince of Wales spruce grouse, with olive underparts and flanks and narrower white tips on the upper tail coverts (Dickerman and Gustafson 1996).

CHAPTER II

HABITAT RELATIONSHIPS OF THE PRINCE OF WALES SPRUCE GROUSE

Introduction

A unique subspecies of spruce grouse, the Prince of Wales spruce grouse (*Falcipennis canadensis isleibi*), occurs only on a few islands in the extreme southern tip of the Alexander Archipelago in southeast Alaska. This temperate rain forest shares few habitat similarities with that of spruce grouse (*F.c. canadensis and F.c. franklinii*) in other areas (Johnsgard 1983, Boag and Schroeder 1992). Inferences on grouse habitat selection patterns in southeast Alaska would be difficult to derive without local habitat-use data. Because spruce grouse have been considered rare in southeast Alaska (Gabrielson and Lincoln 1959, Gustafson 1993), relative to other areas within its range, the need to understand basic habitat-use patterns is heightened (Gustafson 1994). Of particular importance is the management of forested lands within the limited range of spruce grouse in southeast Alaska.

The core spruce grouse population in southeast Alaska occurs on Prince of Wales Island (Gustafson 1994). Northern Prince of Wales island and several surrounding islands comprise the most intensively harvested area of old growth forest in the Tongass National Forest, southeast Alaska (USDA Forest Service 1997). Large expanses of the forest on northern Prince of Wales Island consist of a single, second-growth age class.

For example, much of the high-volume, old-growth forest land (>40%) in the lower, Staney Creek watershed (7,000 ha) was clearcut and is currently in a single age class (20-30 years) (USDA Forest Service 1993). This area exhibits low horizontal diversity when compared with old-growth forests prior to clearcutting. Furthermore, as these stands mature, 70-80 % of the 100-year rotation may be closed-canopy second-growth forest (Alaback 1982). Forage, including forbs and shrubs, is absent from the understory as the stand matures from 30 to 120 years-old, and canopy closure limits epicormic branching (Alaback 1982).

Where scale of habitat selection by spruce grouse can be related to scale of forest management, data from this study will help illuminate effects of anthropogenic fragmentation on spruce grouse populations in southeast Alaska. Isolation of suitable habitat for any species is undesirable within the mandates of the National Forest Management Act (1976), because anthropogenic fragmentation can lead to loss of species viability (Harris 1984, Rolstad 1991, Fahrig and Merriam 1994). In the eastern part of the range, spruce grouse have been unable to occupy suitable habitat patches in the Adirondack Mountains because dispersal distance was too great: patch occupancy decreased linearly as distance to the nearest occupied patch increased (Fritz 1979). Knowledge of habitat suitability and scale of selection across the landscape was needed to determine effects of forest management on spruce grouse populations in southeast Alaska. Furthermore, as information emerges about the distribution of spruce grouse within the landscape of southeast Alaska, biologists will be able to determine the relevance of existing scientific literature from other spruce grouse subspecies.

The primary objective was to describe spruce grouse habitat selection patterns within the temperate rainforest ecosystem of southeast Alaska. To accomplish this objective. I used radio telemetry and the existing Forest Service vegetation database.

Study Area

The Alexander Archipelago, in southeast Alaska, comprises a chain of large islands and thousands of smaller islands. These islands, with thousands of kilometers of rocky and steep shoreline, are separated by a system of seaways including sounds, straits, canals, narrows, and channels. The largest island in the archipelago is Prince of Wales Island which spans 6,900 km^2, and is the third largest U.S. island (Figure 1.1).

Prince of Wales (56°N, 133°W) experiences a cool, moist, maritime climate with precipitation averaging 250 cm annually (NOAA 1990). The moderating influence of surrounding seas creates a narrow temperature range. Mean summer temperature is 20° C and winter temperatures are around 10° C (NOAA 1990). The Coast Mountains, on the mainland, cause a lifting of the airmass which produces abundant moisture (Fitton 1930). Thus, the yearly climate is characterized by cool summers, moderate winters, well-distributed precipitation, heavy snowfall at higher elevations, and a high incidence of cloudiness (300 days/year) (Alaska Climate Center 1986). Daylight ranges from 18.5 to 7.0 hours from summer to winter annually.

The forest of Prince of Wales is a part of the continuous coastal, temperate rainforest along the Pacific rim from northern California to Cook Inlet in Alaska (Harris 1974). The forest of southeast Alaska is predominantly old-growth because of the absence of fire within the ecosystem (Demeo et al. 1992). Other than dispersed large-scale wind events, anthropogenic disturbance is the single most catastrophic (large-scale) agent existing on Prince of Wales Island. Old-growth stands exhibit variable diameters and canopy conditions as well diverse densities of shrubs and forb cover (Demeo et al. 1992). Snags and woody debris are present within these old-growth forest stands. The terrain of southeast Alaska is predominantly steep, rugged, and broken where glaciation scraped areas. Northern Prince of Wales Island, however, is more eroded by glaciation and has more loose till than other islands in the archipelago (Baichtal et al. 1997). Gentle topography and productive soils have made North Prince of Wales the most heavily logged area of the Tongass National Forest (USDA Forest Service 1997).

The forest is a mosaic of stands of various densities, interspersed openings, and large clearcuts. The forest consists of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*) with scattered western redcedar (*Thuja plicata*) and Alaska yellowcedar (*Chameacyparis nootkatensis*) (Alaback 1982). Other common species include red alder (*Alnus rubra*), associated with disturbed areas, and shore pine (*Pinus contorta contorta*), associated with muskegs and other poorly drained sites (Robuck 1985). The most productive, high-volume stands of timber (>3000 m^3/ha) are found near tidewater with stand height and volume usually diminishing as elevation increases.

Interspersed with higher-volume stands are "muskegs" or bog plant communities growing on deep peat and dominated by sphagnum mosses, sedges and rushes, and ericaceous shrubs (Robuck 1985). Tree growth is sparse in muskegs and consists mainly of mountain hemlock (*Tsuga mertensiana*) and shore pine in scrub form. Muskegs help regulate stream flow and provide suitable habitat for many plants with berries consumed by wildlife (Harris and Farr 1974).

Between muskegs and dense forests are more open stands growing on primarily organic soils (Stephens 1969). Tree growth is slow and form is stunted in these stands (Demeo et al. 1992). The resultant open canopy allows sufficient light to reach the forest floor to support dense understory vegetation of blueberry and red huckleberry (*Vaccinium* spp.), rusty menziesia (*Menziesia ferruginea*), and numerous vascular plants (Alaback 1982). Above timberline (800-1,000 m), the alpine zone is dominated by heaths, grasses, and other low plants. Occasional trees occur in shrublike "Krummholz" form (Harris 1974).

The study area for this investigation includes central Prince of Wales Island and eastern Heceta Island (Figure 2.1). These areas span roughly 3,000 km^2. Both areas have extensive logging road networks: mean road density is > 2 km/km^2 (USDA Forest Service, Thorne Bay Ranger District,1998). The area known as Honker Divide (Figure 2.1) was excluded from analysis because I did not attempt to find birds there. This area is the most remote portion of the study area and it would have been difficult and inefficient to monitor birds with radio transmitters. The range of radio transmitters used in this study area was limited to < 1.5 km. Within both islands, the study area was defined as the area within which I searched for birds. Study area delineation was important because random habitat data were selected from within the study area and compared with habitat data from grouse areas. Excluding Honker Divide, which was not

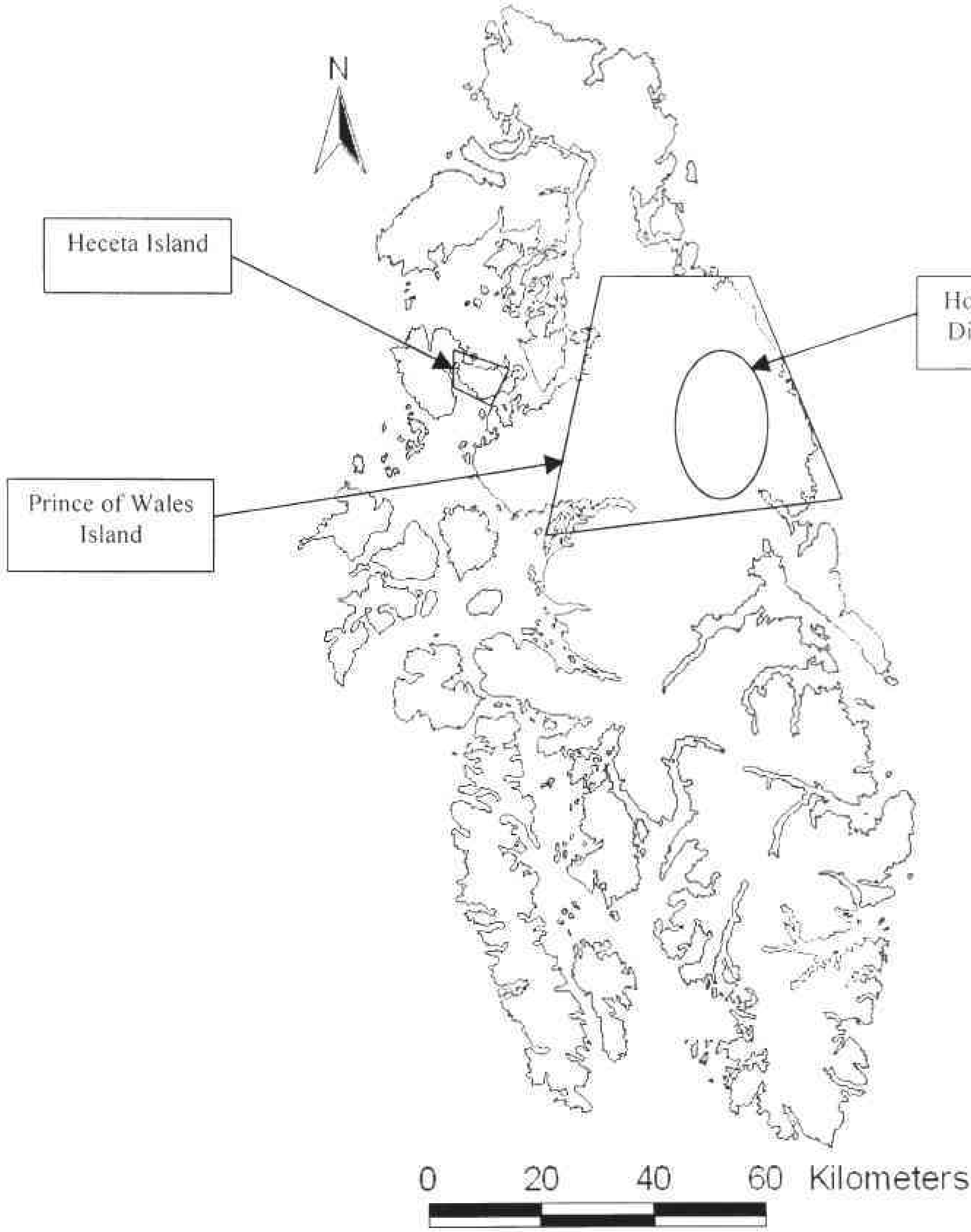

Figure 2.1. Location of study area, Prince of Wales and Heceta Islands, southeast Alaska. The area labeled Honker Divide was excluded from the study area because it was not searched for spruce grouse.

used in the analysis. the areas are similar in forest management history and geomorphic land forms.

Methods

Locating and Capturing Spruce Grouse

Prior to this investigation, documented observations of spruce grouse were infrequent in southeast Alaska (Gustafson 1994). Most sightings were along logging roads. During the course of this investigation. 4 methods were explored to locate spruce grouse (Table 2.1). The "follow-up" method was the only technique that proved time and cost effective. This method required that all Forest Service employees working in the field were aware of the ongoing study and had radios available to call in when spruce grouse were seen. Individuals trained to handle spruce grouse were available to respond quickly to sightings. The observer had to wait and keep constant visual contact with the bird.

Conspecific audio recordings have been reported as an efficient way to locate spruce grouse (McDonald 1968. Fritz 1979. Bouta 1991. Boag and Schroeder 1992). The field crew played tapes of female Franklin's grouse aggressive calls repeatedly in 24 areas where grouse had been observed. From late March through June. I played tapes assuming that females would best respond before the onset of egg-laying (McDonald 1968. Robinson 1980, Bouta 1991. Boag and Schroeder 1992). In addition. on 11 occasions tapes were played immediately following observations of birds (both males and females during the reproductive period).

Table 2.1. Methods of finding spruce grouse on Prince of Wales and Heceta Islands, southeast Alaska, 1996-1998.

Method	*Success Rate*
Conspecific audio recordings: aggressive female vocalization (cantus)	Tapes were obtained for *F.c.frankilnii* and *F.canadensis* and played in known grouse areas (*n*=24) and random areas (*n*=15) to elicit response from male and female spruce grouse. **No positive responses were confirmed**.
Walking transects in areas where grouse had been previously observed.	Field crews walked approximately 40 transects in areas where grouse had been repeatedly observed. **No grouse were encountered with this method.**
Driving logging roads during active brood periods (June, July)	This method was very time consuming and did not prove effective. In approximately 65 hours of driving, **2 brood females were located and one female was captured**.
Follow-up immediately on sightings by USFS employees working on the island.	This method proved most successful. **Twelve of 19 grouse were found this way**. The remaining 7 were located by working with previously radio-tagged birds.

Grouse did not respond to the tapes. In 5 cases, tapes were played while visually observing birds or when capture attempts failed because birds were too high in the tree (e.g., >7 m) and grouse did not respond.

After birds were located, extensible noose poles (*n*=17) and long-handled nets (*n*=2) were used to capture birds. I followed the noose pole design for spotted owl captures (Forsman 1983). Birds were noosed in trees (*n*=8) and on the ground (*n*=11). I attempted to avoid situations with dense vegetation (*n*=1) or where tree limbs prohibited a safe noosing opportunity (*n*=2).

Equipment

Birds were fitted with 9g. necklace-style radio transmitters (RI-2B Holohil Systems Ltd.) which is < 1% of total body mass. Radio transmitters had a life of 14-16 months with no failures. Transmitting distance was approximately 1.6 km but varied according to topography, density of vegetation, and position of the bird. When birds were > 10 m high in trees, transmitting distance exceeded 2 km. Birds found on the ground in sink and swale topographic features transmitted < 1 km.

Using a combination of aerial and ground-based telemetry (from the road system), birds were monitored throughout the year. Birds were monitored intensively during the reproductive period, approximately 3 times per week and less intensively during the remainder of the year (at least 1 relocation per week). Of 987 relocations of 19 radio-tagged birds, 171 were visually confirmed and 22 were aerial locations.

Telemetry Error Estimation

Variable topography potentially introduced a bias in the relocation positions. Telemetry error was initially estimated by placing transmitters in known locations with error polygons calculated accordingly (White and Garrott 1990). Problems with error estimation have been discussed (Nams 1989, Samuel and Kenow 1992, Zimmerman and Powell 1995). Variable topography, density of vegetation, and position of the bird (ground or tree) contributed to error. In addition, position of a road with respect to the grouse home range contributed an additional source of error. I could account for large topographic features and other visible sources of signal bounce, but different areas had more error due to inherent microtopographic features and road positioning relative to the grouse home range.

Initially, I believed that error varied according to the unique topography comprising each grouse home range. To test for differential error or a "site effect," I used a randomized block design with 4 blocks (observers) and 4 treatments (sites). If error varied by site, I felt a separate error estimate would be needed for each grouse home range. Site was not significant ($F_{3,9} = 2.2$, $P > 0.1$), and the grand mean of the sample was used as an error estimate for each relocation in the study. The amount of error in each of 16, independent observations from the telemetry-error experiment was averaged to estimate error. The grand-mean-error-estimate (2 ha) was used for all telemetry including aerial, which was < 1 ha based on the recovery of transmitters from Prince of Wales Island.

Each relocation was buffered with 2 ha circle representing error. The proportion of habitats within the circle provided an estimate of habitat use. The scale at which habitats have been determined for this investigation produces habitat patches > 10 ha in size (USDA Forest Service, Thorne Bay Ranger District, 1998). In addition, no habitat types were considered rare at this scale of habitat delineation. These factors, along with a conservative estimate of error from triangulation, allowed an unbiased estimate of habitat use (i.e., false negative errors should balance false positive errors).

Data Management

Azimuths (vectors), time and location were recorded on radio telemetry data sheets. Polygons were subsequently plotted on aerial photographs. In approximately 105 cases, vector data did not make a closed polygon probably because of error associated with bounce, distance to bird, or vegetation. These data were not used in analyses. On some occasions, increasing the number of vectors resulted in a closed polygon, and previous vectors were discarded (Kenward 1987: 146-150). We used the best (smallest error) 3 or 4 bearings to estimate the polygon (Kenward 1987, White and Garrott 1990). Two vectors were used when a suitable location could not be obtained for a third vector (n=74). Grouse were located 2 times in a 24-hour period on 14 occasions. Otherwise, observations are separated by at least 24 hours and all data points are assumed to be independent (Legendre 1993).

Geographical Information System

To combine and analyze spatial data, centroids from error polygons were entered as a point coverage using a Geographic Information System (GIS) software (ArcInfo 3.0 D+). To analyze data at 3 spatial scales, I used 2 ha buffered-points for location scale and polygons for home range (χ=211 ha) and core areas (χ=34 ha). Results of home range analysis are presented with other natural history data (Chapter IV).

State plane coordinates were imported into the Calhome software program (Kie et al. 1994) for home-range analysis. A 95% utilization distribution was calculated to represent home range, and a 50% utilization distribution was calculated to represent core areas and seasonal home range. Utilization distributions (home range and core-use areas) were imported into Arc/Info as coordinates and home-range polygons were generated.

Using a grid and random numbers, random polygon centroids were selected for comparison with grouse home ranges and core areas. Two random polygons were generated for each grouse home-range polygon. They were located by offsetting the centroid of the grouse home range a random distance within the study area.

Habitat Types and Analysis

Habitat Types

I classified habitats of spruce grouse in order to detect habitat selection patterns. The potential habitats of spruce grouse where divided into 5 vegetation classifications, corresponding to complexity of forest structure (Table 2.2). The first 3 habitats (bog, scrub, and high-volume, old-growth forest, Table 2.2) are natural or unmanaged stands within the larger landscape. The vertical and horizontal structural complexity of these habitats is greater than managed stands (clearcut and second growth), which have uniform, simplified structure.

Table 2.2. Prince of Wales spruce grouse habitat types in southeast Alaska, 1996-1998.

Vegetation Type	*Forest Stand Vegetation* (source: USDA Forest Service, Alaska Region)	*Description of Structural Complexity*
(1) forbs, grass, sedge, and shrubs	muskeg, fen, or **bog** (up to 30% canopy closure)	Mostly ground cover vegetation. Structure is patchy with interspersed trees and shrubs.
(2) forbs, shrubs, and trees	forested wetlands and low-volume forest, **scrub** (<35 CCM[1]/ha 40-50% canopy closure)	Complex structure is present (3-4 layers). Stands usually multi-aged with mixed conifer species and stunted trees. Low live branches and full shrub layer.
(3) forbs, shrubs, and trees	**high-volume, old-growth forest** (>35 CCM/ha, 50-70% canopy closure)	Better drained sites with taller trees and less mid-story canopy (2-3 layers). Shrub and forb layer is patchy depending on canopy closure (> 50%) and gap-phase dynamics.
(4) forbs, shrubs, young conifers, and logging slash	**clearcut** (<15 years old, trees < 5 m tall)	Forest canopy is absent. Openings are usually 250 ha within study area. Shrubs, forbs and slash are abundant (1-2 layers).
(5) conifers	**second growth** (15-30 years, trees > 5m tall)	Forest canopy is approaching closure (1-2 layers). Forbs, shrubs, slash and low live branches are present.

[1] CCM=100 m^3, a measure of timber volume.

Vegetation Maps

Habitat relationships of spruce grouse were evaluated at 3 spatial scales: home range, core area (seasonal home range), and individual locations. At each scale, I compared habitats that grouse used with randomly located habitat in the study area. Random habitats were assumed to be a measure of available habitat at the study area scale of availability (McClean et al. 1998). The Forest Service's GIS database was used to develop vegetation maps of the study area. Spatially referenced vegetation data are used by the Forest Service to estimate volume of timber output anticipated from individual forest stands. By using 2 different combinations of existing vegetation data, I attempted to reduce bias associated with defining habitat as volume of timber and to contrive vegetation maps as suitable analogues of forest structure and grouse habitat.

I used existing Forest Service vegetation data to create vegetation maps (subsequently referred to as "vegetation covers"). These vegetation covers illustrate 2 approaches to defining "habitat" by vegetation structure. Habitat type "other" represents habitats assumed not to be available habitat. Some error from GIS mapping and overlaying is also represented in habitat type "other."

The first vegetation cover emphasizes tree height and canopy closure as measures of forest structure that may be important to spruce grouse (Table 2.3). This approach predicts that habitat selection reflects choice in vertical cover.

Table 2.3. Vegetation Cover I[1] for Prince of Wales spruce grouse habitat in southeast Alaska, 1997.

Forest Type	Tree Height (m)	Canopy Closure	% in Study Area[2]
1 Bog	10	< 30%	10
2 Scrub	20	40 - 50%	20
3 Forest	35	50 - 70%	25
4 Clearcut	< 5	none	10
5 Second Growth	> 5	70 - 100%	20
6 Other[3]	0 - 5	0 - 20%	15

[1]Source: USDA Forest Service GIS database, Thorne Bay Ranger District, Alaska.
[2] Numbers are estimates and are rounded to nearest 5%.
[3] "Other" represents mainly alpine, subalpine, and riparian habitat in this analysis.

The second vegetation cover (Table 2.4) acknowledges a wetland complex and assumes that diverse forest structures (which develop on hydric soils) may be selected by spruce grouse. These habitats are defined by diversity of forest structure as influenced by soil moisture, ranging from open muskeg to high-volume, old-growth forest land.

Table 2.4. Vegetation Cover II[1] for Prince of Wales spruce grouse habitat in southeast Alaska, 1997.

Forest Type	Soil Type	Forest Structure (H, M, L)[2]	% in Study Area[3]
1 Wetland Complex	Hydric	Horizontal diversity (H), Vertical diversity (H)	35
2 High-volume, old-growth forest	Well-drained	Horizontal diversity (M), Vertical diversity (H)	20
3 Clearcut	N/A	Horizontal diversity (L), Vertical diversity (L)	10
4 Second Growth	N/A	Horizontal diversity (L), Vertical diversity (M)	20
5 Other[4]	N/A	N/A	15

[1] Source: USDA Forest Service GIS database, Thorne Bay Ranger District, Alaska.
[2] High, medium, and low rankings interpreted from Demeo et al. (1992).
[3] Numbers are estimates and are rounded to nearest 5%.
[4] "Other" represents mainly alpine, subalpine, and riparian habitat in this analysis.

Data Analysis

To discriminate between used and available resources I used hectares of habitat from the 2 vegetation covers as predictive variables in logistic regression models (Manly et al. 1993). Habitat use was the response variable: "use" = (1) grouse habitat or "use" = (0) random habitat, a measure of availability. Logistic regression is relatively assumption free and proves valuable in exploring small data sets (Hosmer and Lemeshow 1989).

I modeled habitat selection at 3 scales. Individual polygons [location polygons (2 ha) and home range and core area polygons] are classified as either "grouse" or "random." At the point scale, hectares of habitat within each 2 ha polygon were used to predict the response variable "use." The same model was used for home range and core areas. In the location-scale models, data were stratified by bird before pooling. An identifier for each of 19 grouse ("bird-id") was included in the location-scale model. If this variable ("bird-id") was not significant, data were assumed to be independent. Home range and core area models were stratified by bird. I used hectares of habitat in the models because all polygons (case and control at all scales) were of equal size.

I also used logistic regression to evaluate differences between seasonal use (spring/summer vs. fall/winter) because data were too few to break into 4 discrete seasons for analysis. I compared composition of core areas (spring/summer) with home range habitat compositions. I assumed core area was an index of seasonal habitat (spring/summer) use because sampling intensity was 3 times greater during the reproductive period. I used the ranks of "habitats" (because size was not equal) as predictive variables and "seasonal use" as the response variable.

If a significant model was found (at any scale), I attempted to explore multicollinearity of the variables. I deleted each significant variable once from the model in iterations to evaluate changes in significance of the remaining variables. If the results were similar (the same predictive variables were significant), then model coefficients were interpreted.

To illustrate use and availability at 2 scales (location and home range), the percent composition within each grouse polygon (location and home range) was compared to percent composition of random polygons of the same size and shape. I did not illustrate core area habitat compositions because logistic regression results (addressed later) did not indicate that habitat composition of core areas differed from home range.

In addition to the logistic models, I created graphs of percent use of habitats to illustrate the "grouse habitat" and "random habitat" data. Data are not analyzed in univariate tests as these graphs imply because habitat types are not independent.

Results

Logistic regression produced results similar to the patterns exhibited in the percent-use data at the location scale (Figures 2.2 and 2.3). At home range scale,

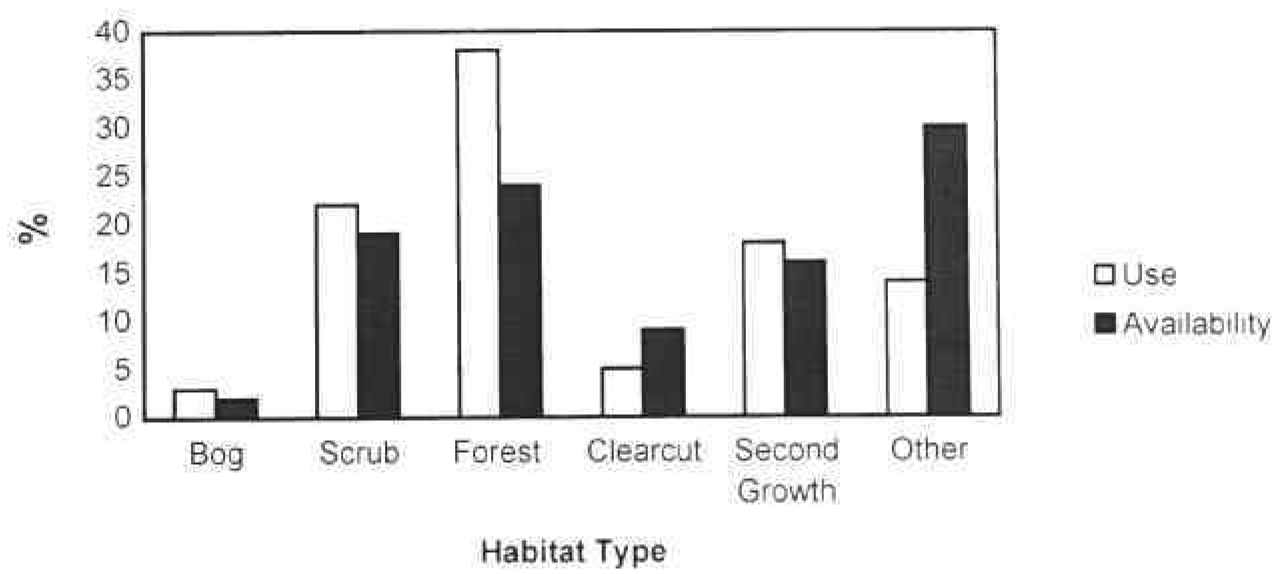

Figure 2.2. Used and available resources at the location scale for spruce grouse in southeast Alaska, 1996-1998--Vegetation Cover I.

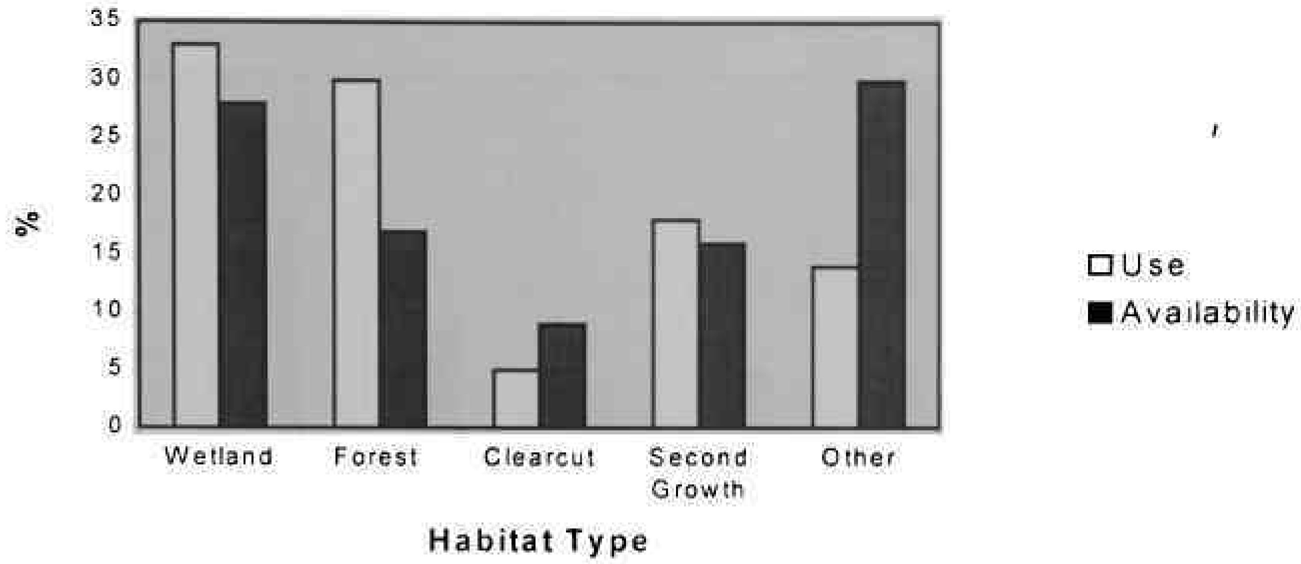

Figure 2.3. Used and available resources at the location scale for spruce grouse in southeast Alaska, 1996-1998--Vegetation Cover II.

however, percent-use data exhibit patterns not found in the logistic models because of variation in habitat use by 13 Prince of Wales spruce grouse with home range estimates (Figures 2.4 and 2.5).

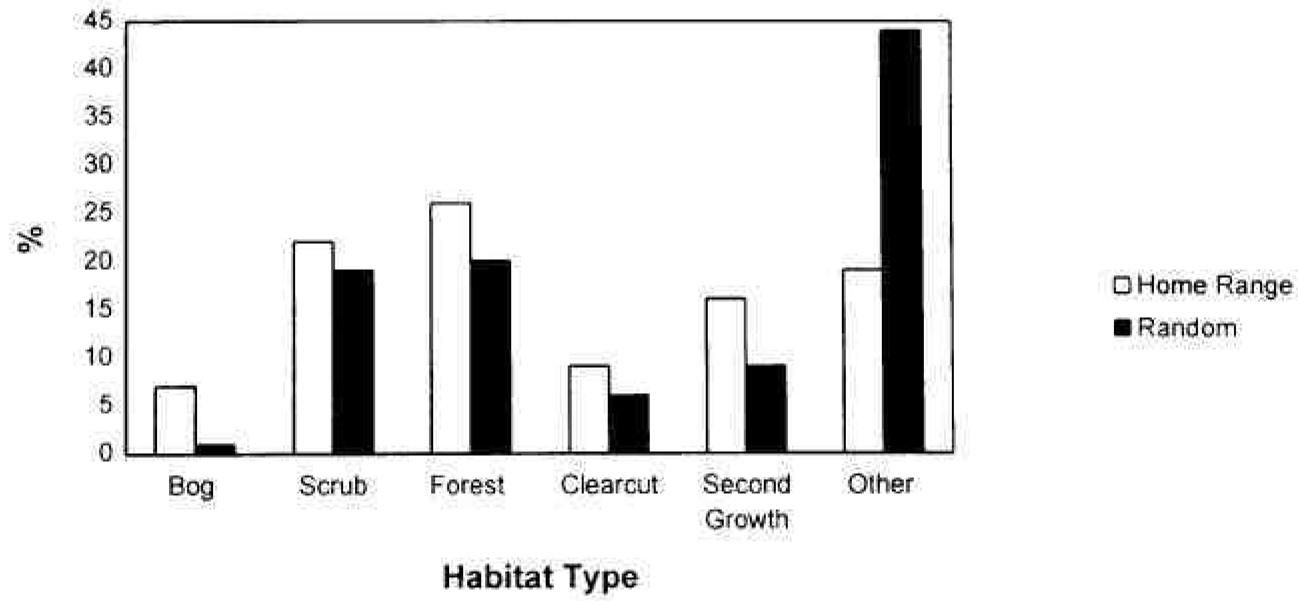

Figure 2.4. Habitat composition in spruce grouse home ranges compared with random polygons in southeast Alaska, 1996-1998--Vegetation Cover I.

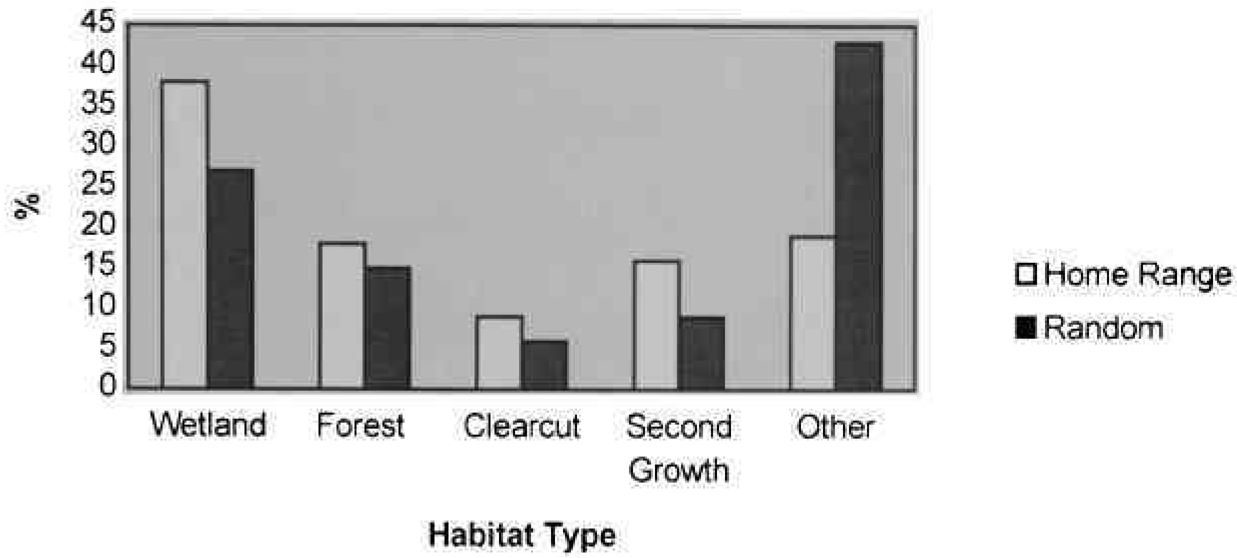

Figure 2.5. Habitat composition in spruce grouse home ranges compared with random polygons in southeast Alaska, 1996-1998--Vegetation Cover II.

At 2 spatial scales (home range and core area) habitat use did not differ from random availability. Using both vegetation covers, I found no significant regressions at the home range ($P > 0.1$ for all habitat variables) or core area scales ($P > 0.1$ for all habitat variables). No models of spring/summer habitat use were significant ($P > 0.1$ for all habitat variables). These results indicate that habitat variables were not good predictors of home range, core area, or spring/summer habitat use. Sample size was small for these models because 13/19 birds had sufficient data (>30 relocations) for home range analysis (Chapter IV).

At the scale of individual location, however, models were fit for vegetation covers I and II indicating that habitat was a good predictor of use and habitat use was non-random. Sample size was larger at this scale because pooled data resulted in 987 independent polygons. "Bird-id" was not significant ($P > 0.1$) indicating that habitat data could be pooled. The model for vegetation cover I is

$$\ln(P) = .20 + .25(x_1) + .10(x_3) - .24(x_4) - .27(x_6)$$

where

$$x_1 = \text{bog},\ x_3 = \text{forest},\ x_4 = \text{clearcut, and } x_6 = \text{other}.$$

The model was significant ($P < 0.01$) and correctly classified 62% of the data. The correct classification of grouse locations is high, 77% (756/987) in vegetation cover I. The selected predictive variables do not account for random points with the same frequency: 47% (465/987). Spruce grouse used scrub and high-volume, old-growth forests most often (Figure 2.2), although scrub was not preferred because use was similar to availability (Table 2.5). Spruce grouse preferred bog and forest but avoided clearcuts.

Table 2.5. Interpretation of coefficients (use vs. availability) for logistic model of habitat selection by spruce grouse in southeast, Alaska 1996-1998--Vegetation Cover I.

Forest Type		P	Coefficient Sign	Habitat Use Pattern
Bog	(x_1)	< 0.01	+	prefer
Scrub	(x_2)	> 0.50	none	as available
Forest	(x_3)	< 0.01	+	prefer
Clearcut	(x_4)	< 0.01	–	avoid
2nd Growth	(x_5)	> 0.50	none	as available
Other	(x_6)	< 0.01	–	avoid

The second vegetation cover revealed similar relationships. When bogs were combined with other wetland habitats, this variable was not a good predictor of habitat use ($P > 0.1$) because availability is widespread within the study area (e.g., Table 2.4). The model for vegetation cover II is

$$\ln(P) = .24 + 0.12(x^2) - 0.25(x^3) - 0.27(x^5)$$

where

x^2 = forest, x^3 = clearcut, and x^5 = other.

The full model was significant ($P < 0.01$) and correctly classified 62% of the data. The correct classification of grouse locations is high (75%, 740/987) for this model (vegetation cover II). Random points are not explained well by the predictive variables: 48%, 472/987 correctly classified. The interpretation of coefficients is similar to the first model, except the wetland habitat is not preferred (Table 2.6). Spruce grouse selected forest habitat and avoided clearcuts.

Table 2.6. Interpretation of coefficients (use vs. availability) for logistic model of habitat selection by spruce grouse in southeast, Alaska 1996-1998--Vegetation Cover II.

Forest Type		P	Coefficient Sign	Habitat Use Pattern
Wetland	(x_1)	> 0.30	none	as available
Forest	(x_2)	< 0.01	+	prefer
Clearcut	(x_3)	< 0.01	–	avoid
2nd Growth	(x_4)	> 0.30	none	as available
Other	(x_5)	< 0.01	–	avoid

Discussion

Habitat selection by Prince of Wales spruce grouse occurred at the finest scale of resolution (individual location). Sample size may have been too small to detect patterns at larger scales. The pattern of use that emerged from this study is in general agreement with selection patterns reported for other subspecies of spruce grouse (Bouta 1991). In addition, these findings support attempts to maintain spatial variation in habitat structure within managed (harvested) forests.

On Prince of Wales Island, mixed-conifer forest (scrub) is widely available. This habitat exhibits substantial use by Prince of Wales spruce grouse and may provide important structural features for avoiding avian and mammalian predators. Mixed-conifer forests are also common components of spruce grouse habitats in other areas, although species composition differs (Robinson 1969, Paterni 1979, Ratti et al. 1984, Allan 1985). Connectivity of scrub and high-volume, old-growth forest within the matrix of managed forest stands may be an important factor in minimizing negative effects to spruce grouse populations in southeast Alaska. Interspersion of habitats creates horizontal diversity, which may be necessary to fulfill the range of spruce grouse life requisites (Boag and Schroeder 1992). A lack of horizontal diversity limited use of large (>150 ha) areas of coniferous habitat by spruce grouse in New York (Bouta 1991).

Prince of Wales spruce grouse did not use clearcuts despite widespread availability. Spruce grouse were found moving around rather than through clearcuts: no evidence of crossing a clearcut was observed despite opportunities for reduced travel distance (Appendix B). Avoidance of this habitat indicates that it is a likely travel and, hence, dispersal barrier. Where contiguous, suitable habitat exists around clearcuts, grouse moved through the contiguous habitat.

Spruce grouse also avoided non-forested areas elsewhere in their range (Boag and Schroeder 1992), although effects of clearcutting *per se* are not well documented. In the Adirondacks, persistently occupied habitats contained a wide range of stand-age classes, suggesting that large clearcuts would be detrimental to habitat suitability (Bouta 1991). Small patch cuts, however, encouraged mixed-species composition and were considered beneficial to horizontal diversity (Bouta 1991). In Minnesota, large-scale clearcutting was thought to extirpate local populations of spruce grouse (Pietz and Tester 1982).

Avoidance of clearcuts by Prince of Wales spruce grouse may be related to several factors. Logging debris (slash) remains after harvest and may hinder movement. Slash can be piled 1-3m high in places, creating uneven walking terrain. Spruce grouse prefer to walk rather than fly between habitats (Boag and Schroeder 1992). Clearcuts also create large openings of uniform structure and reduce horizontal diversity. Clearcuts in my study area were generally 20-60 ha in size whereas natural openings are generally < 10 ha (USDA Forest Service, Thorne Bay Ranger District, 1998) except where they occur in broad expanses on mountain ridge-tops (a habitat not used by spruce grouse in this study). Finally, predation risk, whether real or perceived through relic behavior, may be greater in non-forested areas. Low coniferous cover, low limbs, and ericaceous shrubs all provide concealment from predators (Robinson 1969, Ratti et al. 1983, Boag and Schroeder 1992).

The advent of broad-scale, anthropogenic disturbance (i.e., clearcut logging) is relatively new to this ecosystem: broad-scale forest management was initiated in 1968-1970 in my study area (USDA Forest Service 1993). Clearcuts have more available cover (mostly shrubs and slash) than open muskegs, yet grouse were frequently found in natural openings without shrub or tree cover. Natural openings, which occur in wetland complexes, are smaller than clearcuts and contribute to horizontal diversity. In addition, birds are close to coniferous cover in natural openings. Spruce grouse, especially females, are cryptic within the sphagnum-moss-covered-muskegs, perhaps lessening the need for vegetative cover. The cryptic plumage, combined with stationary behavior when predators are perceived, indicates that avian predation has been a strong selective force in the evolution of spruce grouse life-history characteristics (Johnsgard 1983, Boag and Schroeder 1992).

Grouse were often found in 15-35 year, second-growth stands which regenerate after clearcutting. The density of trees can be virtually impassible to humans with stem density at 2,000 trees/ha. These stands are currently widespread throughout the study area, but will change structure in predictable ways over time. The canopy will completely close and eliminate understory vegetation at approximately 40 years (Alaback 1982). In addition, low limbs will die as sunlight diminishes in the understory. Such homogeneous, mid-successional stages are not yet present within the study area, so my study does not reveal their importance to Prince of Wales spruce grouse. Similar forest structures in the eastern range of spruce grouse are known to be avoided (Bouta 1991).

Although 15-35 year stands were used by Prince of Wales spruce grouse, they were not preferred (through use/availability analysis) in either habitat model. For the percent-use, location data, second growth was used less than high-volume, old-growth forest, scrub, and forested-wetland habitats. In addition, no individual grouse used this habitat exclusively. All grouse that had second-growth forest available within the home range used a combination of second-growth forest with other habitat. These data concur with other research suggesting that spruce grouse select horizontally diverse habitats (Robinson 1969, Robinson 1980, Ratti et al. 1983, Bouta 1991). In addition, risk of avian predators may be greater in young (15-35 years) second-growth forests where horizontal diversity is lower and spruce grouse are more visible from overhead.

In other parts of their range, spruce grouse prefer young successional stands of similar height and stem density to those found in southeast Alaska (McCourt 1969, Haas 1974, Hedberg 1980, Boag and Schroeder 1987, Boag 1991). However, mid-story structure of early successional jack pine and lodgepole pine forests is more persistent than for young forests of Sitka spruce and western hemlock. Young-successional forests in southeast Alaska exhibit relatively ephemeral shrub layers (Alaback 1982, Demeo et al. 1992). Where more open-canopy conditions are created through pre-commercial thinning, a flush of conifer regeneration (especially western hemlock) quickly replaces shrubs (Alaback 1982). Early successional conifer forests in southeast Alaska, therefore, differ structurally from forests of comparable seral stages where spruce grouse exhibit higher densities (McCourt 1969, Boag and Schroeder 1992).

These homogeneous, second-growth stands occur at broad scales within the landscape. Data from this investigation indicate that spruce grouse do not select habitat at such coarse scales as home range and core area--a scale similar to that of managed forest stands. Prior to broad-scale, anthropogenic changes to the landscape in southeast Alaska, old-growth forests occurred in a fine scale-mosaic across the landscape; gap-phase processes, resulting from wind and other disturbances, occur within a matrix of natural fragmentation (Demeo et al. 1992). Thus, the scale at which spruce grouse are selecting habitat in this study is commensurate with the scale of natural forest processes within the ecosystem. Second-growth habitat in southeast Alaska may exhibit characteristics of suitable vertical structure, but it lacks horizontal diversity typical of old-growth forests.

In southeast Alaska, forest structure changes again at approximately 35 years in successional development (Alaback 1982). Within the study area, there are few (<1,500 ha) second-growth stands older than 35 years. Most of the intensive logging (up to 3,000 ha/year) has occurred since the early 1970s on Prince of Wales Island (USDA Forest Service, Thorne Bay Ranger District). Habitat relationships of spruce grouse in older, second-growth forests (> 35 years) remain unclear. The structure of 40-100 year-old forests is markedly different from old-growth stands. Vertical and horizontal structure is simplified and understory vegetation is eliminated (Alaback 1982). Crown closure is approximately 100%, and self-pruning of densely stocked trees reduces low limbs. In the Adirondacks, spruce grouse preferred an interspersion of habitats including saplings, open areas, and mature sites (Bouta 1991). Management activities such as commercial thinning or small patch cuts may encourage structural and horizontal diversity in the managed landscape of southeast Alaska. Moreover, management actions which accelerate development of heterogeneous structures may benefit spruce grouse populations (Robinson 1980, Bouta 1991). Further research is needed to explore the suitability of older, second-growth forest within stands and at the landscape scale in southeast Alaska.

Prince of Wales spruce grouse use of high-volume, old-growth forest was repeatedly observed. On 4 occasions birds were visually located 20-30 m high in the mid-crown of Sitka spruce (Appendix C). Use of the mid-crown may have nutritional advantages for foraging grouse and this portion of the forest canopy provides concealment from avian and terrestrial predators (Boag and Schroeder 1992). Use of mature forests has been documented elsewhere (Aldrich 1963, Ellison 1975, Pietz and Tester 1982). Of all habitats, high-volume, old-growth forest has been most impacted by management activities. Approximately 35% of the high-volume, old-growth forest has been harvested within the study area (USDA Forest Service Thorne Bay Ranger District GIS data, 1998). Spruce grouse may select this habitat on a seasonal basis, although habitat data in this investigation did not support a shift in habitat use between spring/summer and fall/winter. Failure to observe a shift may result from natural fragmentation of the southeast Alaska landscape. Within the study area, all unmanaged habitats were readily available. Spruce grouse would not have to make long-distance movements to shift from use of scrub forest to use of high-volume, old-growth forest seasonally. These habitats are interwoven in the landscape and occur in patches ranging from 10-100 ha (USDA Forest Service, Thorne Bay Ranger District GIS data). Where diverse stand compositions (e.g., horizontal diversity) are present, seasonal movements may not be necessary (Bouta 1991).

High-volume, old-growth forest habitats were selected in both models (vegetation covers I and II) at the location scale. The functional relationship between spruce grouse and this habitat was not studied (e.g., Rosenzweig 1981, Mysterud and Ims 1998). If grouse fitness is tied to availability of high-volume, old-growth forest, information on functional relationships (spatial and temporal) is needed to clarify management implications. Future research may focus on measures of fitness of spruce grouse in landscapes with different habitat compositions.

Management Implications

Prince of Wales spruce grouse populations will likely be reduced by current methods of forest management because grouse selected high-volume, old-growth forest and avoided clearcuts. Availability of scrub forest appears important and possibly sufficient to maintain viable grouse populations, although effects of anthropogenic fragmentation have not been directly tested. Forest-management strategies which consider the landscape mosaic would best serve the long-term viability of spruce grouse in southeast Alaska.

The importance of forest scale, structure, and pattern has permeated the spruce grouse literature from other regions, although results from the entire range of spruce grouse appear, at first, contradictory (Aldrich 1963, Robinson 1969, Ellison 1975, Boag et al. 1979, Robinson 1980, Allan 1985, Pietz and Tester 1982, Redmond et al. 1982, Keppie 1987, Boag and Scroeder 1992). When viewed from the perspective of landscape process, grouse habitat selection patterns appear commensurate with landscape scale (Keppie 1997). In areas with broad-scale disturbance patterns, spruce grouse appear to select habitat at coarse scales (McCourt 1969, Redmond et al. 1982). In contrast, where forest scale is finer, spruce grouse appear to select for horizontal diversity (Bouta 1991).

The temperate rainforest ecosystem of southeast Alaska is a naturally fragmented, horizontally-diverse landscape. Furthermore, forest structure, driven by gap-phase processes, is structurally complex (Demeo et al. 1992). The introduction of broad-scale, anthropogenic disturbance has reduced horizontal landscape diversity. The long-term effects of this change are poorly understood. The forest will not develop structural diversity before it is harvested (regenerated) under current rotation age, 100 years (Alaback 1982, USDA Forest Service 1997). The distribution of managed stands, especially clearcuts, must be considered in the larger landscape so as to limit separation of suitable Prince of Wales spruce grouse habitat. Older second-growth stands (> 35 years) will be structurally different from young forests; research is needed to address these pending habitat relationships.

These data illuminate 3 aspects of Prince of Wales spruce grouse habitat relationships that are of interest to conservation biologists and forest managers. (1) Selection of high-volume, old-growth forest stands by grouse is important. Although the functional underpinnings of this selection are not known, this habitat has been cut at a rapid rate throughout the range of spruce grouse in southeast Alaska. (2) Avoidance of young clearcuts may limit suitable patch occupancy where distance between suitable patches is too great. Clearcuts may be barriers to dispersal where their distribution is widespread within the landscape and where connectivity of suitable habitat is compromised. (3) The value and suitability of older, second-growth stands has not been investigated. Beginning in the next 15-20 years, large expanses of second growth will be in the stem-exclusion stage of seral development (Alaback 1982). The uniform structure of this forest type will not provide horizontal diversity. These stands, however, will exhibit different vertical, structure characteristics than forest types investigated in this study. Data from other studies suggest that these large expanses of homogeneous forest will be unsuitable for spruce grouse, and as a consequence the local distribution of spruce grouse within the study area may contract.

CHAPTER III

REPRODUCTIVE ECOLOGY OF PRINCE OF WALES SPRUCE GROUSE

Introduction

A unique subspecies of spruce grouse, Prince of Wales spruce grouse (*Falcipennis canadensis isleibi*) occurs on a few islands in the temperate rainforests of southeast Alaska. The nearest other spruce grouse subspecies, Franklin's grouse (*F. c. franklinii*), occurs east of the British Columbia Coast Mountains in different habitats (Chapter II, Boag and Schroeder 1992). In order to understand habitat relationships across time and space within the unique, temperate rainforest ecosystem, the functional underpinnings of habitat selection should be established (*sensu* Rosensweig 1981, Mysterud and Ims 1998).

Invertebrates are important for breeding female spruce grouse who require quality food for successful reproduction (Naylor and Bendell 1989). Insects also provide the necessary protein for the early survival of chicks of ground-dwelling birds because protein-rich diets are required during periods of rapid tissue growth (Southwood and Cross 1969, King and Bendell 1982, Baines et al. 1996, Sedinger 1997). Insects comprised the majority of the diet (70%) of newly hatched blue grouse (*Dendragapus obscurus*) and as much as 40% of the diet of 1 month old chicks (King and Bendell 1982). In central Alberta, spruce grouse chicks < 1 week old were reported to exclusively consume arthropods (Pendergast and Boag 1970).

Habitat selection during the early brood period is linked to food and cover requirements (McCourt 1969, DeFranceshi and Boag 1991). Spruce grouse are cryptic within the temperate rainforest of southeast Alaska, perhaps facing a trade-off between foraging and avoiding predators. Availability of a steady source of quality protein, however, may limit production in spruce grouse populations in southeast Alaska. Differences in invertebrate abundance may exist among habitats. For example, a difference in invertebrate abundance has been observed between blueberry-spruce forest and oligotropic bogs in Finland (Stuen and Spidso 1988). Microclimate characteristics of forest openings and bogs that occur in southeast Alaska may provide relatively warmer conditions for invertebrate production than continuous forest (McCourt 1969, DeFranceshi and Boag 1991).

Nest sites and male display areas have been characterized as key habitats within the larger landscape occupied by spruce grouse in other regions (Ellsion 1968, McDonald 1968, Anderson 1973, Keppie and Herzog 1978, Robinson 1980, Redmond et al. 1981, Boag and Schroeder 1992). Nest success has been related to nest concealment (vegetation structure) and other habitat variables (Haas 1974, Keppie and Herzog 1978, Redmond et al. 1981). Low, coniferous cover provides protection from predators at nest sites (Robinson 1969). In Maine, male spruce grouse chose territorial sites with greater canopy closure and tree density than non-territorial sites (Hedberg 1980). Small openings in the otherwise, dense forest canopy provide display sites for males in other regions (Ellison 1968, McDonald 1968, Robinson 1980). In Maine, males chose display sites with greater basal area and lower tree density than random sites (Anderson 1973). Tree density was lower at male-centered plots in Alberta, indicating larger tree diameters at display sites than in surrounding areas (McLachlin 1970).

Based on findings in regions outside southeast Alaska and the inherent vulnerability of birds during the reproductive period, I hypothesized that microhabitats at Prince of Wales spruce grouse nest sites and male display areas would exhibit habitat characteristics that differ from random plots. Differences in forest structure and composition at grouse-centered plots should reveal whether these sites are limiting within the larger landscape. If grouse-selected microhabitats are not different from random, other factors should be investigated to underpin specific habitat relationships during the reproductive period. My objectives were to test for differences in invertebrate abundance among 3 natural habitats and to relate invertebrate abundance to habitat use by brood females. In addition, I measured 3 tree overstory variables (diameter, density, and basal area) at Prince of Wales spruce grouse-centered and random plots to explore microhabitat characteristics of nests and male display areas.

Study Area

Southeast Alaska is a cool, temperate region with coniferous, old-growth forests. Prince of Wales Island is the largest island in the Alexander Archipelago and spans 6,900 km^2. The climate is characterized by annual precipitation (250 cm) and cooler growing seasons than areas farther south (NOAA 1990). Western hemlock-Sitka spruce forests occur below 600m elevation in a mosaic with non-forested (bogs) and forested wetlands (Alaback 1982).

The study area for this portion of the investigation included central Prince of Wales Island, 56°N, 133°W (Figure 2.1). Heceta Island was not included in the study area for this portion of the investigation. Sites sampled for invertebrates and microhabitats occurred within the Prince of Wales study area defined in Chapter II. Telemetry data for brood female habitat use was from central Prince of Wales Island. Invertebrate sampling and microhabitat measurements occurred in grouse home-ranges (Chapter II).

Methods

Invertebrates

I used vacuum netting (Buffington and Redak 1998) to estimate insect abundance among 3 habitats (Table 3.1). This method is superior to other methods such as sweep netting when vegetation height varies among habitats (Cooper and Whitmore 1990). Bog, scrub, and high-volume, old-growth forest were sampled with a D-vac™ because telemetry data indicated that these habitats were used by brood females (Chapter II).

I used a completely randomized experimental design with 3 treatments (habitats) and 5 replications (15 total sites) to examine habitat differences in invertebrate biomass. Fifteen sites were randomly selected from a larger set of homogenous of experimental units. All potential sites were selected at similar elevation, slope, topography, and soils. Sites were selected such that all 3 habitats occurred adjacent to one another. I did not sample closer than 80 m between habitat types, to avoid possible edge effects (Concannon 1995). Six of the 15 sites sampled were in areas where brood

Table 3.1. Habitats used by female Prince of Wales spruce grouse with broods in old-growth forest of southeast Alaska, 1996.

Vegetation Type	Forest Stand Vegetation (source: Forest Service GIS database)	Description of Structural Complexity
(1) forbs, grass, sedge, and shrubs	muskeg, fen, or *bog* (up to 30% canopy closure)	Mostly ground cover vegetation. Structure is patchy with interspersed trees and shrubs.
(2) forbs, shrubs, and stunted trees	forested wetlands and low-volume forest, *scrub* (<35 CCM/ha[1] 40-50% canopy closure)	Complex structure is present (3-4 layers). Stands usually multi-aged with mixed-conifer species. Low live branches and full shrub layer.
(3) forbs, shrubs, and tall trees	*high-volume, old-growth forest* (>35 CCM/ha, 50-70% canopy closure)	Better drained sites with taller trees and less mid-story canopy (2-3 layers). Shrub and forb layer is patchy depending on canopy closure (> 50%).

[1] CCM = $100m^3$, a measure of timber volume.

females were known to be active through radio-telemetry and visual observations. Using the D-vac [tm], an invertebrate vacuum machine, I collected 10 samples within each of the 15 (n=5, with 3 treatments) sites. Sub-samples were collected by sampling at 10 equally spaced locations (10 m apart) along a transect line. Transects were randomly located within each habitat type. Nine sites were sampled in June, 1996 and 6 sites were sampled in June, 1997. I attempted to sample all 15 sites in 1996 but heavy rainfall prohibited equipment use.

Samples were immediately labeled and frozen. Each sub-sample (fresh mass) was weighted to the nearest 0.001 g. Fresh mass was used because of the relatively small mass of the samples. Means were generated from sub-samples to yield a more robust estimate of abundance at each site. If differences were not found in invertebrate biomass among habitats, I conducted *a posteriori* power analysis, because this experiment marks the first investigation of its type in southeast Alaska (Steidl et al. 1997). No data were available for *a priori* power analysis.

Brood Female Habitat Use

To relate invertebrate abundance to habitat use by brood-rearing females (brood females), I examined percent use of 3 habitats by 4 brood females during June and July. Brood females were captured with extensible noose poles (Forsman 1983) and fitted with 9-g. necklace style transmitters similar to Bouta (1991). Radios comprised less than 1% of the total body mass. Birds were radio-tracked using ground based and aerial telemetry. Triangulation error was estimated in a separate experiment (Chapter II). A 2-ha polygon surrounds each relocation and was used to calculate habitat use. To meet the objective of relating habitat use to invertebrate abundance, I examined percent use of the habitats measured for invertebrate abundance (Table 3.1).

I used analysis of variance (ANOVA) to analyze differences in the dependent variables (bog, scrub, forest). Habitat types in this analysis do not sum to 1 and are assumed to be independent. If differences in habitat use occurred ($P<0.05$), least squares mean separation tests were conducted.

Microhabitats

To investigate forest structure at grouse nest sites and male display areas, I used the "stand exam" method (USDA Forest Service, Pacific Northwest Region 1989). The Forest Service uses this variable-radius plot method throughout southeast Alaska to characterize overstory timber volume and structure of forest stands. This method allowed use of existing Forest Service stand exam data for random plots throughout the study area. There were 6 nests, 5 male display areas, and 30 random plots measured in this investigation. Nests and male display areas were generally located by following previously radio-tagged birds (9 of 11). One nest and 1 male display area were found prior to radio-tagging the birds.

The following data were collected for all tree species to characterize structure and composition at grouse-centered and random plots: diameter at breast height, trees/ha, and basal area. Data were collected in variable-radius plots using a Spiegal relaskop with a 10-factor basal-area prism (USDA Forest Service 1989).

The 3 variables were correlated and sample size was too few to meet assumptions of multivariate analysis (Dunteman 1984). Plot means were cross-referenced to the *Forest Plant Association Guide* (Demeo et al. 1992) for analysis. Means from grouse-centered and random plots were used to classify each plot type according to a vegetation zone and vegetation series (Figure 2.2). Each series provides information about structure and composition of forest understory and overstory characteristics.

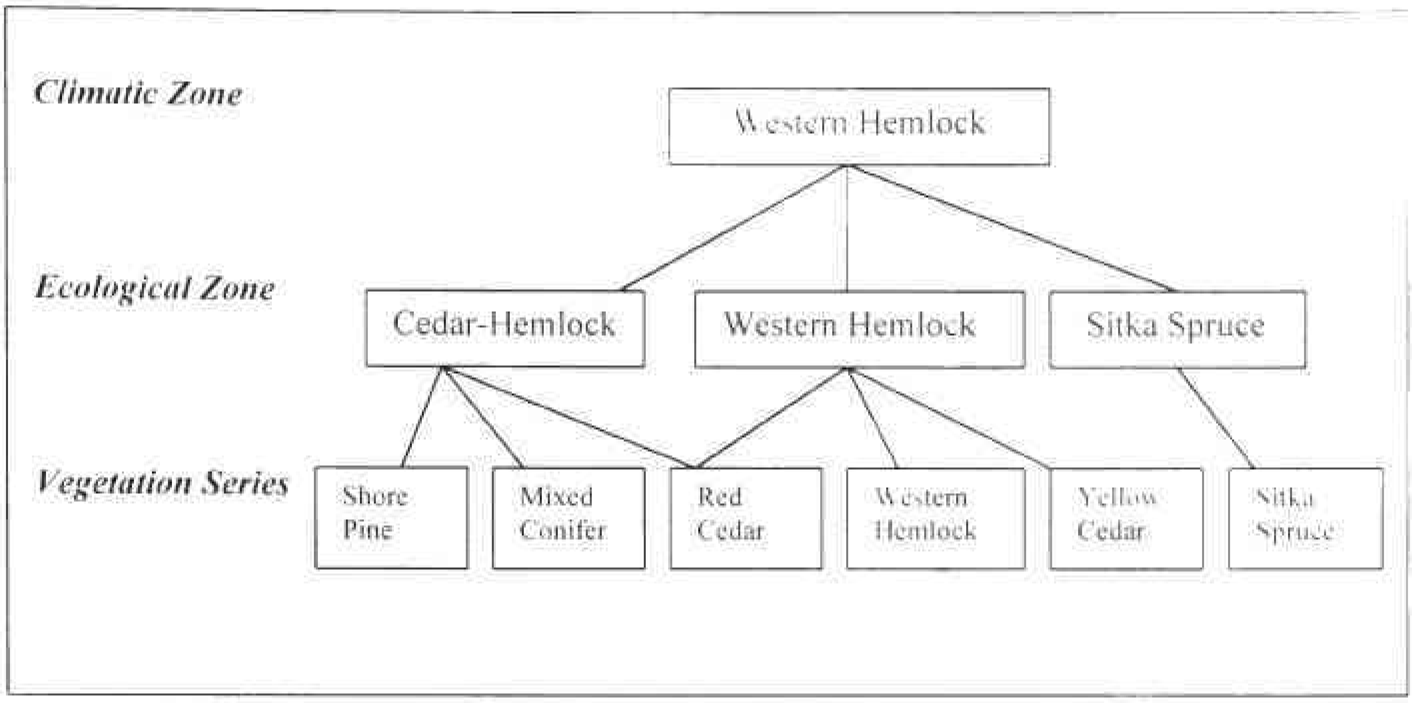

Figure 3.1. Hierarchical forest ecosystem classification, Tongass National Forest, Alaska.

The Plant Association (PA) *Guide* is a synthesis of data from 1,000 vegetation/soils/timber plots (500 m^2) that allows comparison with stand exam data from grouse microhabitats and random plots. I used tree species composition data from grouse microhabitats to classify each plot type into a vegetation series (Figure 3.1). Vegetation series comprise information on forest structure, including overstory and understory, forbs and shrubs. In addition I used 4 Student's independent t-tests to determine if random plots differed from nests and male display sites, respectively in total tree density and total basal area (for all tree species combined).

Results

Invertebrates

The distribution of invertebrates was patchy within habitats and no treatment (habitat) differences were detected ($F_{2,12} = 1.75$, $P > 0.1$). Within-site variability ($SS_{error} = 0.23$) was greater than between site variability ($SS_{treatment} = 0.07$). Mean abundance was not higher in the scrub habitat type: $\chi = 0.35g \pm 0.07$ vs. $\chi = 0.2g \pm 0.06$ in the other 2 habitats, bog and high-volume, old-growth forest.

Habitat use by 3 of 4 brood females exhibits a pattern consistent with invertebrate abundance (Figure 3.2). There were overall differences in brood female habitat use

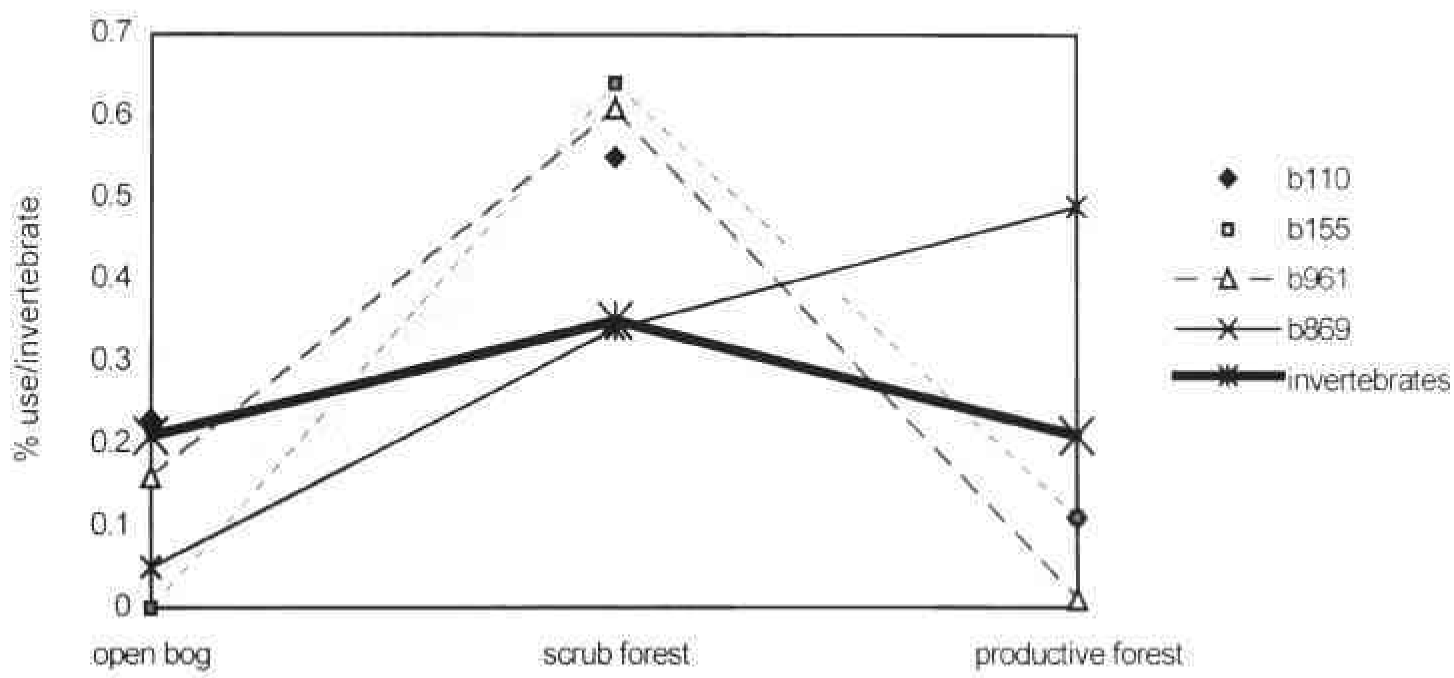

Figure 3.2. Pattern of brood female habitat use plotted with invertebrate biomass in 3 habitat types for Prince of Wales spruce grouse in southeast Alaska 1996-1997.

($F_{2,9} = 8.3$, $P<0.01$). Subsequent analysis revealed that brood females used scrub forest more often ($\chi = 0.5 \pm 0.07$) than the other habitat types ($\chi = 0.1 \pm 0.05$ for bog, $\chi = 0.2 \pm 0.1$ for high-volume, old-growth forest). In order to relate the results of brood female habitat use to invertebrate abundance, more power was needed in the invertebrate research design (Power = 0.28). To achieve a power of 0.75, 37 replications would be needed.

Microhabitats

Overstory tree species composition for nests, display sites, and random plots occurred in the "cedar-hemlock ecological zone." This zone occurs along a continuum of soil drainage: the mixed-conifer series is poorly drained, whereas the western hemlock-western redcedar series is somewhat poorly to well drained (Demeo et al. 1992).

Male display areas were on poorly drained sites and occurred in the "mixed-conifer" vegetation series. These sites featured an open canopy with approximately 45% cover. A dense shrub layer (40% cover) of *Vaccinium* occurred in the midstory along with stunted conifers. Female nest sites and random plots occurred in a transition series of the cedar-hemlock ecological zone. Canopy conditions were more closed with a mean cover of 60%. Less light through the forest canopy reduces shrub development: *Vaccinium* cover was 30%.

Male display sites had a higher density of tree species that grew on poorly drained sites (i.e. mountain hemlock, *Tsuga mertensiana*: Figure 3.3). When all tree species were combined, male display sites differed from random plots in tree density (t = 2.35, 34df, $P<0.05$) but not basal area (t= 1.49, 34df, $P>0.1$). Tree density and basal area were not different (t=1.14, 35df, $P>0.1$; t=1.41, 35df, $P>0.1$) between nest sites and random plots.

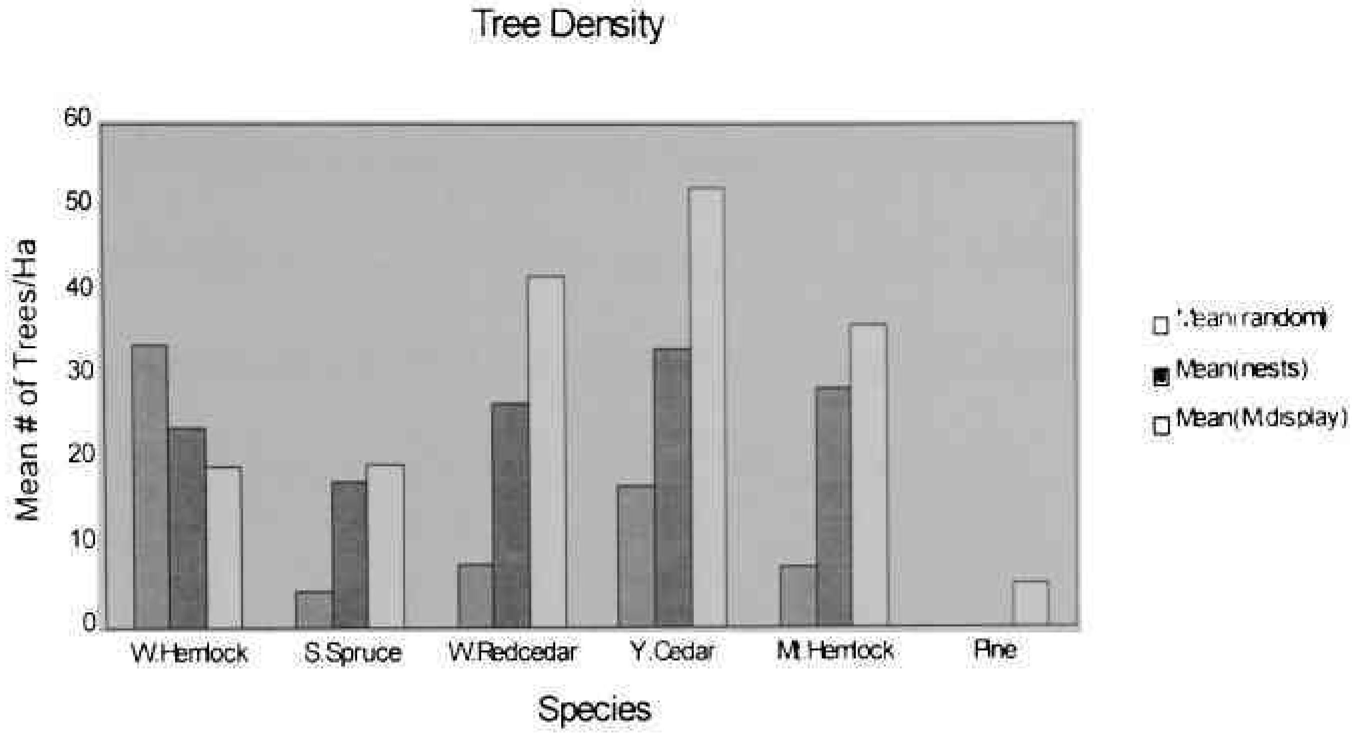

Figure 3.3. Trees/ha by species for spruce grouse microhabitats (female nests and male display areas) and random plots in southeast Alaska 1996-1998.

Discussion

Invertebrates

This study was the first investigation of invertebrate abundance related to gallinaceous birds in southeast Alaska. Furthermore, terrestrial invertebrate research in general has been limited in southeast Alaska. Research questions have focused on pest management or food resources for anadromous and resident fish (USDA Forest Service 1997). Results of *a posteriori* power analysis indicate a more intensive sampling design that accounts for variation in invertebrate abundance and activity may be needed to detect differences among habitats.

A weak pattern emerged in the relationship between invertebrate abundance and brood female habitat use in scrub forest. Scrub forest may provide important food and cover resources for brood females. Relatively open canopy conditions, characteristic of this forest type, create diverse structural characteristics. High vertical and horizontal diversity may allow for increased light, warmth, and foliage for invertebrates. Spruce grouse females with broods chose more open canopy conditions than broodless females in southwest Alberta and Maine (McCourt 1969, Hedberg 1980). Brood-rearing habitat for many grouse species has centered around forb and shrub cover where insects and other protein-rich foods are present (Bergerud 1988, Sveum et al. 1998).

Microhabitats

Male Prince of Wales spruce grouse display areas occurred in stands with less canopy closure and higher tree density than random sites. This open canopy structure may be suited to characteristics of the "wing-clap" courtship display, unique to Prince of Wales spruce grouse in southeast Alaska (Chapter IV). Males confine courtship displays to the trees and do not use forest openings as described elsewhere (McDonald 1968, Robinson 1980). Males may have selected sites with open forest canopy and dense mid-story cover for better concealment from predators (Robinson 1980, Boag and Schroeder 1992). Higher total tree density at male display sites may provide concealment from avian and mammalian predators (Ratti et al. 1984). These display sites, characterized by the mixed-conifer vegetation series, are widespread in the study area (e.g., Table 2.3) and are not usually among forest types selected for timber harvest (i.e. scrub forest, Table 2.2) (Demeo et al. 1992).

Forest structure and composition at nest sites were similar to random plots and fell within the same vegetation series. Nest concealment may be less important in southeast

Alaska, because all habitat types examined (nest and random sites) exhibited dense vegetation and cover. Random sites and nest sites had the same tree density and basal area, and exhibited robust shrub layers that would likely provide adequate concealment if that was the most important factor governing nest success (Keppie and Herzog 1978, Redmond et al. 1982). Other factors, such as habitat variables or landscape pattern that could influence predator activity near nests may be of equal or greater importance to nest success (D'Eon 1997). Factors influencing predator activity near nests may considered for future research in southeast Alaska. Nest sites and random plots occurred in forest types that would be considered for timber harvest (Demeo et al. 1992). Because of tree species composition, however, nests sites were generally in areas of lower economic viability than random sites (Demeo et al. 1992, USDA Forest Service 1997).

The scale of measurement may be too coarse to adequately characterize selection patterns in the reproductive ecology of Prince of Wales spruce grouse. Measurements on a finer scale may be needed to address underlying relationships of habitat selection. More likely, these sites (display areas and nest sites) are probably so widespread within this ecosystem that selection is not apparent. If measurements were taken at an appropriate scale to detect selection, I did not observe characteristics of nests or display areas that could be considered unique or limiting within the forest of southeast Alaska. Although male display sites were in areas of higher tree density, the vegetation series (mixed-conifer) is widespread in the study area (Demeo et al. 1992).

In summary, several studies have examined functional underpinnings of habitat-use patterns (Nicholson et al. 1997, Mysterud and Ims 1998). In such studies, it is assumed that foraging habitat and escape habitat are spatially segregated. In southeast Alaska some evidence has emerged to suggest that scrub forest habitat may provide a favorable composition of patches comprising food and cover during the reproductive period. Brood females and invertebrates exhibited a pattern of selection for this habitat type. In addition, scrub forest may be a preferred habitat for courtship display. Scrub forest exhibits diverse vertical structure and occurs in a fine-scale mosaic with high-volume, old-growth forests (Demeo et al. 1992). This pattern on the landscape exhibits high horizontal diversity (Chapter II), which has been a key habitat characteristic of spruce grouse habitat in some regions (Bouta 1991).

Scrub forest may exhibit key characteristics for reproduction while high-volume, old-growth forest remains an important habitat component for other life requisites (Chapter II). As examined in this portion of the study, habitat selection during the reproductive period represents 1 aspect of life-history characteristics at 1 scale of selection (e.g., Johnson 1980). Studies which go farther to examine aspects of fitness (production and recruitment in this case) relative to habitat use at multiple scales will do more to contribute to our understanding of the functional underpinnings of habitat selection in spruce grouse.

CHAPTER IV

NATURAL HISTORY OF PRINCE OF WALES SPRUCE GROUSE

Introduction

A geographically and genetically isolated subspecies of spruce grouse (*Falcipennis canadensis isleibi*) inhabits a few islands in the Alexander Archipelago in southeast Alaska. The exact distribution of this subspecies is unknown. The first observations of the subspecies were in 1905 (Osgood 1905), and Swarth (1911) compiled evidence of spruce grouse on several islands. The Alexander Expedition was the first to document the allopatric distributions of blue grouse (*Dendragapus obscurus*) and these spruce grouse in southeast Alaska (Swarth 1911). The majority of islands in the Alexander Archipelago, the adjacent mainland, and the Queen Charlotte Islands to the south are inhabited by blue grouse but lack Prince of Wales spruce grouse (Gustafson 1994).

The glacial history of southeast Alaska offers an explanation for the isolated distribution of Prince of Wales spruce grouse. These spruce grouse may have been isolated from other populations for 10,000 years due to remote glacial refugia. Evidence for glacial refugia has emerged from scientific inquiries of the past decade (Putnam and Fifield 1995, Heaton 1996, Heaton et al.1996, Heaton and Grady 1992, Heaton et al. 1996). During the last glacial maximum (Wisconsin 17,000 years before present), sea level may have been about 130 m lower than it is today (Baichtal et al. 1997).

Waterways, former barriers to dispersal, were eliminated or constricted throughout the extreme southern portion of the archipelago. Deep ice receded approximately 12,000 years BP and waterways again interrupted the connectivity of the region. Fossils of spruce grouse from caves in Virginia date the occurrence of this species at least to the Wisconsin glaciation, although the species is clearly much older (Wetmore 1962)

Perhaps as a consequence of long-term isolation, this subspecies of spruce grouse exhibits morphometric characteristics distinct from other spruce grouse subspecies (Dickerman and Gustafson 1995). No field studies had been previously conducted to observe Prince of Wales spruce grouse in southeast Alaska. Although originally described as the Franklin's grouse (Osgood 1905, Swarth 1911, Gabrielson and Lincoln 1959), no documented evidence of the wing-clap display, characteristic of that race, had been observed. In addition, no other courtship displays had been previously observed. In this chapter, I report home range data, an estimate of density, and descriptive natural history data on male courtship displays. Other than limited morphology data, the scientific literature currently lacks any information on Prince of Wales spruce grouse (Dickerman and Gustafson 1996).

Study Area

Southeast Alaska is a cool, temperate region with coniferous, old-growth forests. Prince of Wales Island is the largest island in the archipelago and spans 6,900 km^2. The climate is characterized by heavy annual precipitation (250 cm) and cooler growing seasons than areas farther south (NOAA 1990). Western hemlock-Sitka spruce forests occur below 600m elevation in a mosaic with non-forested (bogs) and forested wetlands (Alaback 1982).

The study area for this portion of the study includes central Prince of Wales Island, 56°N, 133°W (Figure 2.1). Home range data and observations of male courtship displays occurred within the study areas of Prince of Wales Island and Heceta Island defined in Chapter II (Figure 2.1).

Methods

Home Range

I attempted to find and radio-tag as many Prince of Wales spruce grouse as possible for home range analysis. Spruce grouse were difficult to find, however, and were located for capture most frequently by incidental observations from forest workers (Chapter II). Grouse were captured primarily with extensible noose poles and fitted with necklace-style transmitters similar to Bouta (1991). Transmitting distance was approximately 1.6 km. Nineteen spruce grouse were captured and radio-tagged between spring 1996 and fall 1997.

Radio locations were obtained primarily from the road system (n=774, relocations from triangulation) and supplemented with visual observations (n=171) and aerial telemetry (n=22). Grouse were located approximately 3 times per week in spring/summer and 1 time per week during fall/winter. Grouse were located 2 times per day on 14 occasions, otherwise observations for individual grouse are separated by at least 24 hours. Location data were assumed to be independent because of their temporal separation (Legendre 1993, Hansteen et al. 1997).

Centroids from error polygons were entered into GIS and a coverage of grouse coordinates was imported into the Calhome program (Kie et al. 1994) for home-range analysis. The adaptive kernel method was used with the estimated optimum bandwidth (Worton 1989, Kie et al. 1994). The bandwidth is a smoothing parameter. A least squares cross-validation score was used to determine how well the bandwidth fitted the data (Kie et al. 1994). Smaller bandwidths were investigated, but I found polygons were breaking up where bimodal distributions occurred (e.g., 2 separate core areas).

The area/observation curve investigated by Kenward (1992) for animals with different-sized home ranges revealed that 30 points were needed to approximate the 100% utilization distribution. A 95% utilization distribution was calculated for 13 of 19 birds with sufficient data (>30 points) to estimate home range. The 50% utilization distribution (core area) represents the spring/summer home range, because sampling intensity was 3 times greater during the reproductive period.

Male Courtship Display

I observed male courtship displays in April and May in order to determine the type of display used (i.e., wing claps or flutter flights). For this investigation, all behavioral observations followed *ad libitum* sampling methods (Altman 1974). I did not attempt to quantify frequency of behavior and sampling intervals were not predetermined. The primary objective was to record as many display events as possible during nonsystematic sampling periods. Observations were recorded to illustrate type of courtship display exhibited by the Prince of Wales spruce grouse. I used observations of courtship behavior to distinguish between the "flutter flight" of *F.c. canadensis* or "wing-clap" of *F.c. franklinii* (McDonald 1968, Harju 1971). As initial data, these observations can be used to plan systematic behavior sampling.

Results

Home Range

The mean home range estimate for adult birds in this study was 211 ha (SD=71). Males and female home ranges did not differ ($F_{1,11}$=1.2, P>0.1; Figure 4.1). Home range configurations of adjacent birds were not exclusive, but overlap did not exceed approximately 25 % in this study. One adult female and an adult male shared 25% overlap of home ranges annually.

Spring/summer home ranges were estimated using a 50% utilization distribution (Figure 4.4). The mean size of seasonal home range was 34 ha (SD = 12 ha). There was no difference in seasonal home ranges of males and females ($F_{1,11}$=1.4, P>0.1; Fig 4.2). Two males (1 adult, 1 juvenile) shared 20% overlap within their seasonal home ranges.

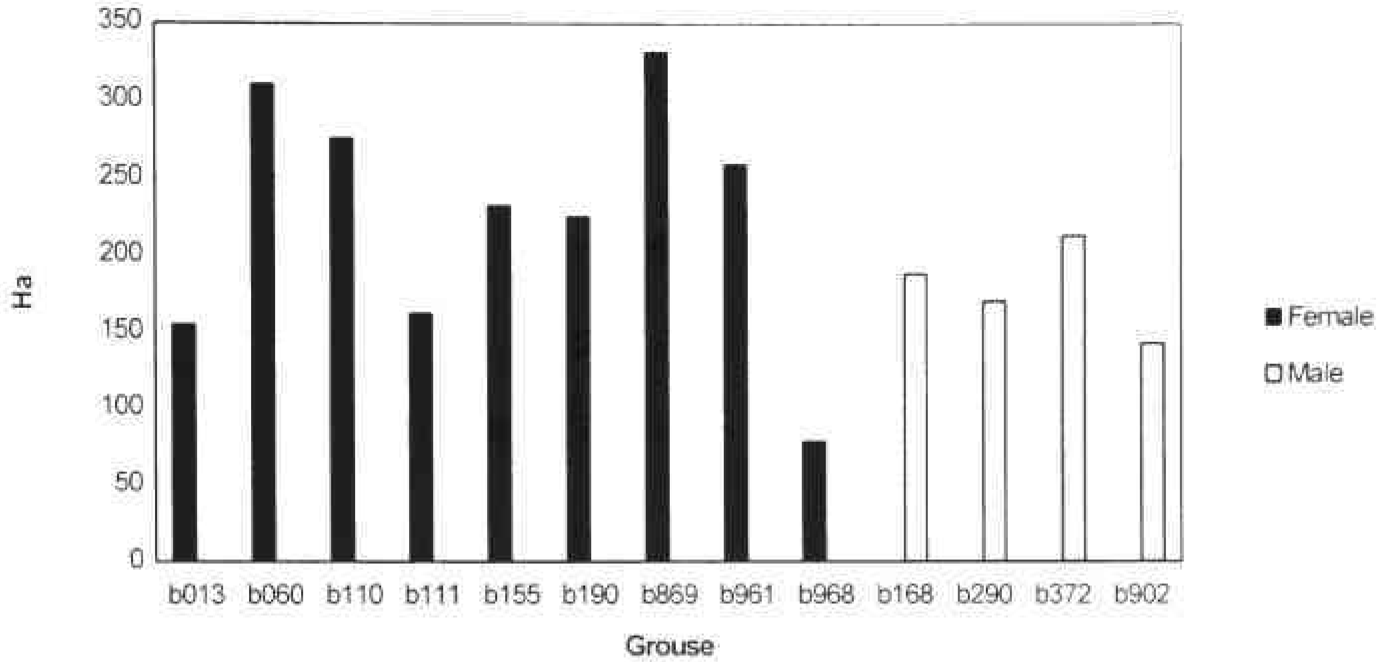

Figure 4.1. Home range estimates (95% utilization distribution) for adult and yearling, male and female spruce grouse in southeast Alaska 1996-1998.

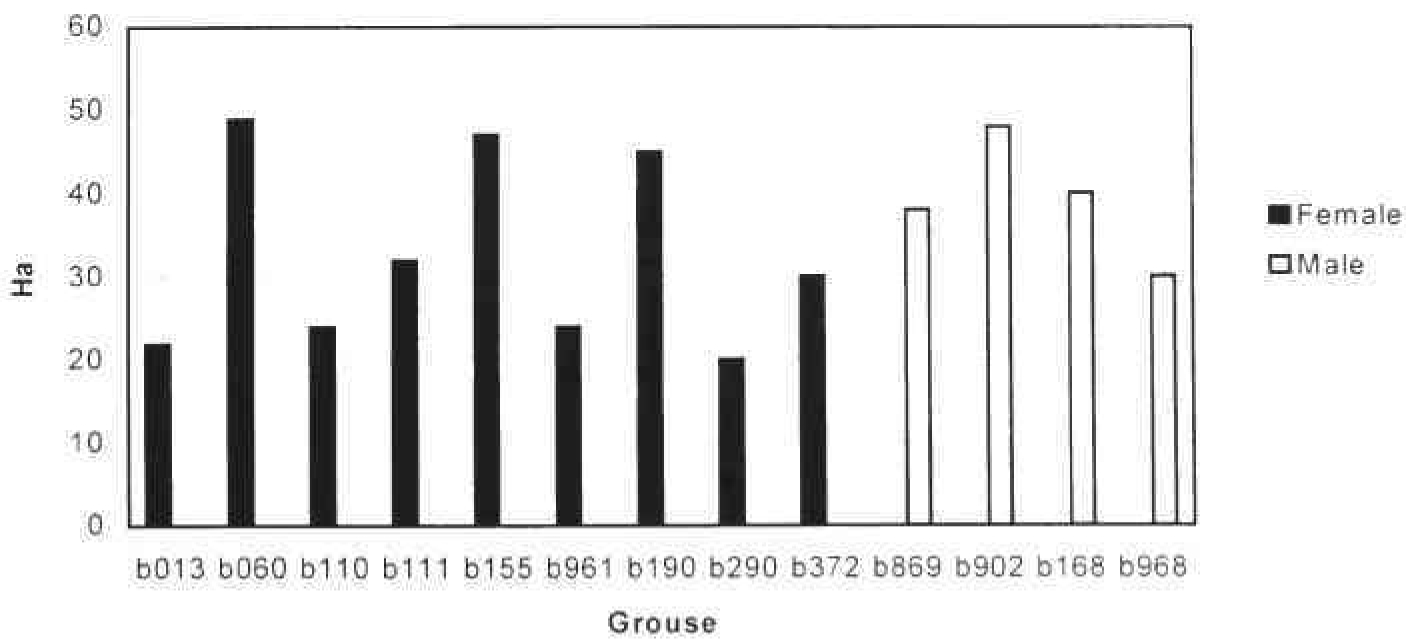

Figure 4.2. Spring/summer home range estimates (50% utilization distribution) for adult and yearling, male and female spruce grouse in southeast Alaska 1996-1998.

Based on home range estimates and available habitat, an approximate population-size estimate can be derived for Prince of Wales Island, southeast Alaska:

[(total hectares)(0.6 proportion available habitat)] / [(home range)(0.8 overlap)]

[(720,000 ha)(0.6)] / [(34 ha)(0.8)] = @ 10,500 spruce grouse.

Available habitat was estimated as an extension of available habitat in the study area (Table 2.3). Habitats considered unavailable include clearcuts (10%), alpine and subalpine (20%), and an additional 10% unavailable resulting from isolation and other factors. Seasonal home range (spring/summer) is represented by the 50% utilization distribution, which may reflect territorial boundaries thought to be exclusive (Keppie 1987, Bouta 1991). I observed approximately 20% overlap and increased the estimate accordingly. This density estimate (2.5 birds/100 ha of available habitat) is likely low, but it is the only estimate with supporting data.

Male Courtship Display

I observed the breeding display behavior of 5 male grouse on 17 separate occasions from 10 April to 9 May. A variation of the "wing-clap" display, characteristic of Franklin's grouse, was observed (McDonald 1968, Harju 1971). I did not observe the "wing-stroke" display or "drumming-like" behavior (McDonald 1968). Males flew 15-20m from a 10m high branch on 1 tree to a branch of similar height on another tree and wing-clapped twice in flight. Males did not fly to a clearing on the ground as a routine part of the wing-clap display (McDonald 1968). I observed a noticeable pause in mid-air as the wings were brought together over the back. Each time males were observed, they clapped twice in flight. The volume of sound produce by the clap was variable. One of the 2 claps was usually louder than the other, but audibility was generally poor. At the loudest, I speculated that it could be heard from 50 m through dense vegetation. The smallest volume of sound could be heard from only 20-40 m.

Males were observed wing-clapping at dawn and dusk, with peak (12 of 17) display before official sunrise (04:00 Alaska Standard Time in mid-April). On 2 occasions, I observed males displaying during the afternoon; the intensity of this display was less than during morning hours. Males rarely flew to the ground (n=2). Feather display, strutting, and pecking occurred in the tree. Aggressive male displays were not observed, and no females were observed in the vicinity of displaying males. No copulation activity was observed. Males did not respond to playback recordings of aggressive Franklin's grouse females nor did they respond to imitated claps. I did not observe use of downed logs for displays.

Discussion

Results of home range size and configuration analysis indicate that spruce grouse occupy larger home ranges in southeast Alaska than in other parts of their range (Boag and Schroeder 1992). Although data are relatively few (13 individuals for home-range analysis), they indicate that this population exists at low densities. The hypothesis of low densities is also supported by the paucity of documented sightings (Gustafson 1994) and lack of territorial interactions observed. Failure to detect birds has likely led to bias in estimating density because overlap may have exceeded the observed estimate. While obtaining 171 visual observations, we observed unmarked birds within the seasonal home range of radio-tagged birds on only 3 occasions. Spruce grouse are difficult to detect in the temperate rainforest of southeast Alaska because of dense vegetation. Based on the difficulty of visually spotting radio-tagged birds, I believe that more birds may have been present than I was able to detect (Chapter II).

Spruce grouse are at the margin of their range in southeast Alaska. Similar to other species, they exhibit densities lower than in the center of the range. Low densities are the likely result of a synergistic effects of proximate factors: low recruitment, low immigration, mortality (Appendix A). The above density estimate is low compared with estimates for New Brunswick. Densities of 6-10/100 ha are reported at the eastern edge of spruce grouse range (Keppie 1987). However, the ability to detect birds in southeast Alaska is hindered by vegetation density. The use of well-trained dogs for finding birds warrants further investigation (Keppie 1987).

McDonald (1968) documented display behaviors of Franklin's grouse; data presented here include noteworthy deviations from that account. Vegetation density may preclude ability of male grouse to make the extensive wing-strokes that McDonald (1968) observed in southwest Alberta. Poor audibility of the Prince of Wales grouse wing-clap display both in volume (relative to that described elsewhere) and reduced audibility from dense vegetation seems to result in a change in the nature of the display: it does not appear to announce positioning. There are several possible explanations for the differences in the male courtship displays between Prince of Wales spruce grouse and Franklin's grouse: (1) founder effects from a small population (i.e., genetic drift);

(2) adaptations to the dense vegetation of the temperate rainforest; and (3) selection due to other species (competition and predation).

Evolution following a founding event has been more closely linked to differences in environment than genetic drift (Whitlock 1997). In addition to differences in environment, food resources, competition, and predation affect optimum phenotype (Schluter and Grant 1984). The Prince of Wales spruce grouse occurs on only a few islands in southeast Alaska. These islands comprise different sizes and species assemblages (e.g., MacArthur and Wilson 1967). Therefore, selection pressure not only differs across the range of spruce grouse in the form of competition, predation, parasitism and food, but also within the islands of southeast Alaska. The different environment of southeast Alaska could translate into substantial phenotypic changes, such as those observed in this investigation (Appendix D) and by Dickerman and Gustafson (1996).

LITERATURE CITED

Alaback, P.A. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology 63: 1932-1948.

Alaska Climate Center. 1986. Technical Note No.3. Alaska Department of Natural Resources. Anchorage, AK.

Aldrich, J.W. 1963. Geographic orientation of American tetraonidae. Journal of Wildlife Management 27: 529-545.

Allan, T.A. 1985. Seasonal changes in habitat use by Maine spruce grouse. Canadian Journal of Zoology 63: 2738–2742.

Anderson, L.J. 1973. Habitat use, behavior, territoriality, and movements of the male Canada spruce grouse of northern Minnesota. Master's thesis. University of Minnesota, St. Paul, MN. 119pp.

Altman, J. 1974. Observation study of behavior: sampling methods. Behaviour 49: 227-269.

Baichtal, J., G. Streveler, and T. Fifield. 1997. The geological, glacial and cultural history of southern southeast. Alaska Geographic: Alaska's southern panhandle 24: 6-31.

Baines, D., I.A. Wilson, and G. Beeley. 1996. Timing of breeding in Black Grouse *Tetrao tetrix* and Capercaillie *Tetrao urogallus* and distribution of insect food for the chicks. Ibis 138: 181-187.

Bergerud, A.T., and M.W. Gratson. 1988. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press. St. Paul, MN. USA.

Boag, D.A. and M.A. Schroeder. 1992. Spruce Grouse. *in* A. Poole, P. Stettenheim, and F. Gill, editors. The Birds of North America, No.5. The Academy of Natural Sciences, Philadelphia, Washington D.C.

---------------and------------------. 1987. Population fluctuations in Spruce Grouse: what determines their number in spring? Canadian Journal of Zoology 65: 2430-2435.

Boag, D.A., K.H. McCourt, P.W. Herzog, and J.H. Alway s. 1979. Population regulation in spruce grouse: a working hypothesis. Canadian Journal of Zoology 57: 2275-2284.

Bouta, R.P. 1991. Population status, historical decline, and habitat relationships of spruce grouse in the Adirondacks of New York. Master's thesis, State University of New York, Syracuse, NY. 119pp.

Buffington, M.L. and R.A. Redak. 1998. A comparison of vacuum sampling versus sweep-netting for arthropod biodiversity measurements in California coastal sage scrub. Journal of Insect Conservation 2:10-15.

Concannon, J.A. 1995. Characterizing, structure, microclimate, decomposition of peatland, beachfront, and newly logged forest edges in southeast Alaska. PhD. dissertation, University of Washington, Seattle, WA. 430pp.

Copper, R.J., and R.C. Whitmore. 1990. Arthropod sampling methods in ornithology. Studies in Avian Biology 13: 29-37.

Defranceschi, P.F., and D.A. Boag. 1991. Summer foraging by spruce grouse: implications for galliform food habits. Canadian Journal of Zoology 69: 1707–1711.

D'Eon, Robert G. 1997. Vegetative concealment, proximity to trails, and predator activity as relative factors affecting nest success and egg loss in Spruce grouse, *Dendragapus canadensis*. Canadian Field-Naturalist 111: 399-402.

Demeo, T., J. Martin, and R.A. West. 1992. Forest plant association management guide. Ketchikan area, Tongass National Forest. R10-MB-210.

Dickerman, R.W. and J. Gustafson. 1996. The Prince of Wales spruce grouse: a new subspecies from southeastern Alaska. Western Birds 27: 41-47.

Dunteman, G.H. 1984. Introduction to multivariate analysis. Sage, Beverly Hills, CA.

Ellison, L.N. 1966. Seasonal foods and chemical analysis of winter diet of Alaskan spruce grouse. Journal of Wildlife Management 30: 729-735.

--------------. 1972. Role of winter food in regulating numbers of Alaskan spruce grouse. Ph.D dissertation, University of California, Berkeley, CA. 171pp.

--------------. 1973. Seasonal social organization and movements of Alaskan spruce grouse. Condor 75: 735-385.

--------------. 1974. Population characteristics of Alaskan spruce grouse. Journal of Wildlife Management 40: 383-395.

--------------. 1975. Density of Alaskan spruce grouse before and after fire. Journal of Wildlife Management 39: 468-471.

Fahrig, L., and G.Merriam. 1994. Conservation of fragmented populations. Conservation Biology 8:50-59.

Fitton, E.M. 1930. The climates of Alaska. Monthly weather revision 58: 85-103.

Forsman, E.D. 1983. Materials and methods for locating and studying spotted owls. USDA Forest Service general technical report, Pacific northwest-12: 1-8.

Fritz., R.S. 1979. Consequences of insular structure distribution and extinction of Spruce grouse populations. Oecologia 42: 57-65.

Gabrielson, I.N. , and F.C. Lincoln. 1959. Birds of Alaska. The Wildlife Management Institute, Washington D.C., USA.

Gurchinoff, S., and W.L. Robinson. 1972. Chemical characteristics of jack pine needles selected by feeding spruce grouse. Journal of Wildlife Management 36: 80-87.

Gustafson. J.E. 1993. The Franklin's spruce grouse in Alaska. Unpublished report. Alaska Department of Fish and Game, Ketchikan, AK. 9pp.

-----------------, 1994. The Franklin's grouse of southern Southeast Alaska. Unpublished report. Alaska Department of Fish and Game, Ketchikan, Alaska. 20pp.

Haas, G.H. 1974. Habitat selection, reproduction, and movements in female spruce grouse. Ph.D. dissertation, University of Minnesota, Minneapolis, MN. 121pp.

Hanley, T.A. 1993. Balancing economic diversity, biological conservation and human culture: the Sitka black-tailed deer as an ecological indicator. Biological Conservation 66: 61-66.

Hansteen, T.L., H.P. Andreassen, R.A. Ims. 1997. Effects of spatiotemporal scale on autocorrelation and home range estimators. Journal of Wildlife Management 61: 280-290.

Harju, H.J. 1971. Spruce grouse copulation. Condor 73: 380-381.

Harris, A.S. 1993. The forest ecosystem of southeast Alaska, no.1: The setting. USDA Forest Service general technical report, Pacific northwest 12: 8-25.

-------------. 1974. The forest ecosystem of southeast Alaska, no.1: The setting. USDA Forest Service general technical report, Pacific northwest 12: 14-19.

Harris, A.S., and W.A. Farr. 1974. The forest ecosystem of southeast Alaska, no.7: Forest ecology and timber management. USDA Forest Service general technical report, Pacific northwest 25: 14-19.

Harris, L.D. 1984. The fragmented forest: island biogeography theory and the preservation of biotic diversity. University of Chicago Press, Chicago, IL.

Harrsion, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42:73-88.

Heaton, T.H. 1996. The late Wisconsin vertebrate fauna of On Your Knees Cave, northern Prince of Wales Island, southeast Alaska. Journal of Vertebrate Paleontology 16: 40A-41A.

Heaton, T.H., and F. Grady 1992. Two species of bear found in late Pleistocene/ early Holocene den in El Capitan Cave, Prince of Wales Island, southern Alaska coast. Journal of Vertebrate Paleontology 12: 32A.

Heaton, T.H., S.L. Talbot, and G.F. Shields. 1996. An ice age refugium for large mammals in the Alexander Archipelago, Southeastern Alaska. Quaternary Research 46: 186-192.

Hedberg, J. 1980. Habitat selection by spruce grouse in eastern Maine. Master's thesis, University of Maine, Oron, ME. 63pp.

Herzog, P.W. , and D.A. Boag. 1977. Seasonal changes in aggressive behavior of female spruce grouse. Canadian Journal of Zoology 55: 1734-1739.

------------------and-------------. 1978. Dispersion and mobility in a local population of spruce grouse. Journal of Wildlife Management 42: 853-865.

Herzog, P.W., and D.M. Keppie. 1980. Migration in a local population of Spruce grouse Condor 82: 366-372.

Hohf, R.S., J.T. Ratti, and R. Croteau. 1987. Experimental analysis of winter food selection by spruce grouse. Journal of Wildlife Management 51: 159-167.

Hosmer, D.W., and S. Lemeshow. 1989. Applied logistical regression. John Wiley & Sons, New York, NY.

Johnsgard, P.N. 1983. The grouse of the world. University of Nebraska Press, Lincoln, NE.

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65-71.

Kenward, R. 1987. Wildlife radio tagging: equipment, field techniques, and data Analysis. Academic Press, London, U.K.

Kenward, R.E. 1992. Quantity versus quality: programmed collection and analysis of radio-tracking data. Pages 231-246 *in* I.G. Pride, editor. Wildlife telemetry: remote monitoring and tracking of animals. Ellis Horwood, New York, NY.

Keppie, D.M. 1979. Dispersal, overwinter mortality, and recruitment of spruce grouse. Journal of Wildlife Management 43: 717-727.

---------------. 1982. A difference in production and associated events in two races of spruce grouse. Canadian Journal of Zoology 60: 2116-2123.

---------------. 1987. Impact of demographic parameters upon a population of spruce grouse in New Brunswick. Journal of Wildlife Management 51: 771-777.

---------------. 1997. Fragmentation of spruce grouse *Dendragapus canadensis* habitat: a synthesis of the present and direction for the future. Wildlife Biology 3: 284.

Keppie, D.M., and P.W. Herzog. 1978. Nest site characteristics and nest success of Spruce grouse. Journal of Wildlife Management 42: 628-632.

Keppie, D.M. and J. Towers. 1990. Using phenology to predict commencement of nesting of female spruce grouse *(Dendragapus canadensis)*. American Midland Naturalist 124: 164-170.

Kie, J.G., J.A. Baldwin, and C.J. Evans. 1994. Calhome. Home Range Analysis Program. Los Angeles, CA.

King, R.D., and J.F. Bendell. 1982. Foods selected by blue grouse *(Dendragapus obscurus fuliginosus)*. Canadian Journal of Zoology 60: 3268-3281.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology 74: 1659-1673.

MacDonald, S.D. 1968. The courtship and territorial behavior of Franklin's race of spruce grouse. Living Bird 7: 5-25.

Manly, B., L. McDonald, and D. Thomas. 1993. Resource selection by animals. Statistical design and analysis for field studies. Chapman and Hall, London, UK.

McCarther. R.H., and E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press. Princeton, NJ.

McClean, S.A., M.A. Rumble, R.M. King. and W.L. Baker. 1998. Evaluation of resource selection methods with different measures of availability. Journal of Wildlife Management 62: 793-801.

McCourt, K.H. 1969. Dispersion and dispersal of female and juvenile Franklin's grouse in southwestern Alberta. Master's thesis, University of Alberta. Edmonton. 130pp.

McLachlin, R.A. 1970. The spring and summer dispersion of male franklin's grouse in lodgepole pine forest in southwestern Alberta. Master's thesis. University of Alberta, Edmonton. 153pp.

Mysterud. A., and R. A. Ims. 1998. Functional responses in habitat use: Availability influences relative use in trade-off situations. Ecology 79: 1435-1441.

Nams, V.O. 1989. Effects of radio-telemetry error on sample size and bias when testing for habitat selection. Canadian Journal of Zoology 67: 1631.

Nams, V.O., and S. Boutin. 1991. What is wrong with error polygons? Journal of Wildlife Management 55: 172.

National Oceanic and Atmospheric Administration, National Weather Service, and NCDC. 1961-1990. Alaska monthly precipitation. cloudiness. relative humidity, and wind. Anchorage, AK.

Naylor, B.J., K.J. Szuba, and J.F. Bendell. 1988. Nest cooling and recess length of incubating Spruce Grouse. Condor 90: 489-492.

Nicholoson, M.C., T. Bowyer, and J.G. Kie. Habitat selection and survival of mule deer: tradeoffs associated with migration. Journal of Mammalogy 78: 483-504.

Nugent. D.P., and D.A. Boag. 1982. Communication among territorial spruce grouse. Canadian Journal of Zoology 60: 2624-2632.

Osgood. W.H. 1903. Smithsonian Institute Archives. Rec. Ut. 7176. Bx. 13. Fld. 17. U.S. Fish and Wildlife Service, 1860-1961. Washington D.C., USA.

----------------. 1905. In Alaska's rain belt. Condor 7: 68-71.

Paterni. M.J. 1979. Winter habitat selection by female spruce grouse in a mixed coniferous forest. Master's thesis, University of Montana. Missoula. 96pp.

Pendergrast, B.A., and D.A. Boag. 1970. Nutritional aspects of the diet of Spruce grouse in central Alberta. Condor 73: 437-443.

Pickett, S.T.A., and P.S. White. 1985. Natural disturbances and patch dynamics: an introduction. Pages 1-9 *in* S.T.A. Pickett and P.S. White, editors. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press. Orlando. FL.

Pietz. P.J., and J.R. Tester. 1982. Habitat selection by sympatric spruce and ruffed grouse in north central Minnesota. Journal of Wildlife Management 46: 391-403.

Putman, D.E., and T. Fifield. 1995. Estuarine archaeology and holocene sea-level change on Prince of Wales Island, Alaska. *in* Proceedings of " Hidden Dimensions": the cultural significance of wetland archaeology. Vancouver. British Columbia, Canada.

Ratti, J.T. . D.L. Mackey, and J.R. Allredge. 1984. Analysis of spruce grouse habitat in north-central Washington. Journal of Wildlife Management 48: 1188-1196.

Redmond, G. W., D.M. Keppie, and P.W. Herzog. 1982. Vegetative structure, concealment, and success of nests of two races of spruce grouse. Canadian Journal of Zoology. 60: 670-675.

Robinson, W.L. 1969. Habitat selection by spruce grouse in northern Michigan. Journal of Wildlife Science 33: 113-120.

Robinson, W.L. 1980. Fool hen. The spruce grouse on the Yellow Dog Plains. University Wisconsin Press, Madison, WI

Robuck, O.W. 1985. The common plants of the muskegs of southeast Alaska. USDA Forest Service, Pacific Northwest Forest and Range Experiment Station. Portland, OR.

Rolstad, J. 1991. Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. Biological Journal of the Linnean Society 42: 149-163.

Rosenzweig. M.L. 1981. A theory of habitat selection. Ecology 62: 327-335.

Saltz. D., and G.C. White. 1990. Comparison of different measures of error in simulated radio-telemetry locations. Journal of Wildlife Management 54: 169-174.

Samuel. M.D., and K.P. Kenow. 1992. Evaluating habitat selection with radio-telemetry triangulation error. Journal of Wildlife Management 56: 725.

Schluter, D., and P.R. Grant. 1984. Determinants of morphological patterns in communities of Darwin's finches. American Naturalist 123: 175-196.

Schroeder, M.A., and D.A. Boag. 1985. Behavior of spruce grouse broods in the field. Canadian Journal of Zoology 63: 2494-2500.

---------------------and------------- 1991. Spruce grouse populations in successional lodgepole pine. Ornis Scandinavia 22: 186-191.

Sedinger, J.S. 1997. Adaptations to and consequences of an herbivorous diet in grouse and waterfowl. Condor 99: 314-326.

Southwood, T.R.E., and D.J. Cross. 1969. The ecology of partridge. III. Breeding success and the abundance of insects in natural habitats. Journal of Animal Ecology 38: 497- 509.

Steidl, R. J., J.P. Hayes, and E. Schauber. 1997. Statistical power analysis in wildlife research. Journal of Wildlife Management 61: 270-279.

Stephens, F.R. 1969. Source of cation exchange capacity and water retention in southeast Alaskan spodosols. Soil Science 108: 429-431.

Stoneberg, R.P. 1967. A preliminary study of the breeding biology of the Spruce grouse in Northwestern Montana. Master's thesis, University of Montana, Missoula. 120pp.

Stiling, Peter D. 1992. The causes of population change. Pages 230-232 *in* Sheri L. Snavely, senior editor. Ecology: Theories and applications. Prentice-Hall, Upper Saddle River, NJ.

Stuen, O.H. and T.K. Spidso. 1988. Invertebrate abundance in different forest habitats as animal food available to Capercaillie *Tetrao urogallus* chicks. Scandinavian Journal of Forest Resources 3: 527-532.

Swarth, H.S. 1911. Birds and mammals of the 1909 Alexander Alaska Expedition. University of California Publication. Zoology 7: 9-172.

Sveum, C.M., J.A. Crawford, and W.D. Edge. 1998. Use and selection of brood-rearing habitat by sage grouse in south central Washington. Great Basin Naturalist 58:344-351.

Szuba, K.J. and J.F. Bendell. 1983. Population densities and habitats of Spruce grouse in Ontario. Pages 199-213. *in* R.W. Wein. R.R. Riewe. and I.R. Methuen. editors. Resources and dynamics of the boreal zone. proceedings of a conference. Thunder Bay, Ontario, August 1982. Association of Canadian Universities for Northern Studies, Ottawa. Canada.

U.S. Department of Agriculture. The Forest Service. 1983. Final environmental impact statement: LPK timber sale plan for the 1984-85 operating period. Tongass National Forest, Alaska. Alaska Region Report Number 170.

------------------------. 1997. Tongass Land Management plan revision. Supplement to the draft environmental impact statement. R-10-MB -145.

------------------------. 1993. Central Prince of Wales final environmental impact statement: Ketchikan Pulp Company long-term timber sale contract. R-10-MB-229a.

U.S. Department of Agriculture, The Forest Service, Pacific Northwest Region. 1989. Stand exam program: field procedure guide. Portland, OR.

Wetmore. A. 1962. Notes on fossil and subfossil birds. Smithsonian Misc. Collection 145: 1-17.

White. G.C., and R.A. Garrott. 1990. Analysis of wildlife radiotracking data. Academic Press, San Diego, CA.

Whitlock. M.C. 1997. Founder effects and peak shifts without genetic drift: adaptive peak shifts occur easily when environments fluctuate slightly. Evolution 51: 1044-1048.

Worton. B.J. 1989. Kernal methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168.

Zimmerman., J.W., and R.A. Powell. 1995. Radiotelemetry error: location error method compared with error polygons and confidence ellipses. Canadian Journal of Zoology 73: 1123-1133.

APPENDIX A

SURVIVAL ESTIMATES AND PROBABLE CAUSES

OF MORTALITY FOR PRINCE OF WALES SPRUCE GROUSE,

1996-1998, SOUTHEAST ALASKA

Survival

Annual survival was calculated for adult and yearling grouse that were radio-tagged between 1 May and 15 July and still alive on 1 May the following year (Keppie 1987). I used the Kaplan-Meier product limit to estimate annual survival (Lee 1996). Data among age-classes are pooled similar to Keppie (1987). Annual survival for 17/19 adult and yearling grouse was 45% (±0.11).

Differences in survival among the subspecies of spruce grouse have been documented (Ellison 1974, Keppie 1979, Boag et al. 1979, Keppie 1987). Franklin's grouse (*Falcipennis canadensis franklinii*) exhibited high survival rates (67.5%) in southwest Alberta (Boag et al. 1979). In New Brunswick and south-central Alaska, spruce grouse (*Falcipennis canadensis canadensis*) survival was 47% and 30%, respectively (Ellison 1974, Keppie 1987).

Mortality

Causes of mortality were determined by carefully examining the site where the radio transmitter was recovered (Table A.1). In 2 of 9 mortality events, approximately 2-4 weeks elapsed before cause of mortality was determined. In these cases (1 raptor and 1 mammal suspected), I estimated the probable cause of mortality based on condition of the remains.

Table A.1. Probable causes of mortality of adult, yearling, and juvenile (post-dispersal) Prince of Wales spruce grouse, 1996-1998, southeast Alaska.

Causes of Mortality	*Number of birds*
Goshawk (head torn off, feathers plucked)	2 (adults)
Marten, ermine or wolf (feathers chewed)	2 (one yearling, one adult)
Hit by car (found dead by road side)	2 (one yearling, one adult)
Shot by hunters (reported)	2 (one juvenile, one adult)
Research related (stress during handling)	1 (adult)
total	9 (*n*=19 for the study)

APPENDIX B

DISPERSAL DISTANCE AND PATTERN FOR 3 SIBLING PRINCE OF WALES SPRUCE GROUSE, 1996-1997, SOUTHEAST ALASKA

Dispersal

Measures of dispersal have limited inference, as all 3 juveniles in this study were siblings. Mean dispersal distance was 1.8 km (n=3, 2/3 female). This distance compares with average dispersal distance (2.0 km) found by Schroeder (1986) in southwest Alberta.

Dispersal pattern was noteworthy: none of the juveniles moved through young clearcuts. The brood area occupied by the 3 radio-tagged siblings was bordered on 2 sides (north and east) by clearcuts (0-10 years). Juvenile birds moved either west (n=1) or south (n=2). Habitats moved through included scrub forest and productive forest. Bogs occur in small-scale patches within a matrix of scrub forest indicating that this habitat type (bog) may have been used also.

Additionally, birds moved for a longer period of time than is reported for fall dispersal (Beaudette and Keppie 1992). Fall dispersers typically settle into a winter range for arboreal feeding by early December (Schroeder 1985). Radio-tagged juveniles in this study did not appear to settle into a home range (characteristic of 10 adult birds) until early spring (March) of the following year. This pattern is consistent with spring dispersal of spruce grouse Keppie (1979).

APPENDIX C

DIET OF PRINCE OF WALES SPRUCE GROUSE, 1996-1998,

SOUTHEAST ALASKA

Diet

During this study, 4 birds were examined after being struck by automobiles (2 of the birds were radio-tagged). Crops from all 4 birds contained Sitka spruce (*Picea sitchensis*) buds and needles. In addition, crops containing Sitka spruce needles were found at two kill sites, where the predator was assumed to be goshawk. Spruce grouse were observed eating Sitka spruce, western hemlock (*Tsuga heterophylla*), and *Vaccinium spp.* during the study.

Juvenile birds had begun to eat conifer needles, Sitka spruce and western hemlock, by approximately 8 weeks old. Southeast Alaska is the only region within the range of spruce grouse where birds consume Sitka spruce and western hemlock. The nutritional ecology of these species has not been investigated.

APPENDIX D

MORPHOLOGY, CLUTCH SIZE, NESTING CHRONOLOGY OF PRINCE OF WALES SPRUCE GROUSE, 1996-1998, SOUTHEAST ALASKA

Morphology, Clutch Size, and Nest Chronology

I collected weight and wing chord data for 12 19 spruce grouse (Table D.1). Wing chord data were collected when circumstances permitted longer handling time (8/12). Brood females were released as quickly as possible to facilitate brood care. When weather was severe (rain and wind) we released birds as quickly as possible and did not obtain measurements (7/19).

Table D.1. Weight and wing chord measurements for Prince of Wales spruce grouse, 1996-1998, southeast Alaska.

Bird	*wing chord (mm)*	*weight (g)*
adult male (902)		580
adult male (372)		560
adult male (090)	178	595
juvenile male (290)	172	600
juvenile female (130)	171	480
juvenile female (961)		420
juvenile female (869)		480
adult female (155)	174	495
adult female (road kill)	175	
adult female (013)	187	551
adult female (968)	176	487
adult female (111)	189	570

Wing chord measurements compare with *F.c. franklinii* and are generally longer than those recorded for *F.c. isleibi* (Dickerman and Gustafson 1996).

I collected clutch size, nest chronology, and nest success data. Three nests had 6 eggs and 2 nests had 5 eggs. Average clutch size for Franklin's grouse was 4.8 (Keppie 1982). Egg-laying begins the last week in April based on evidence from 3 nests. No nests were depredated in this study ($n = 6$) based on observations of eggshell fragments. Two nests (yearling) were abandoned following long incubation times.

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